Fishery Bulletin

Vol. 86, No. 2 April 1988

PEARCY, WILLIAM G., and JOSEPH P. FISHER. Migrations of coho salmon, *Oncorhynchus kisutch*, during their first summer in the ocean 173
DUTIL, J.-D. and J.-M. COUTU. Early marine life of Atlantic salmon, *Salmo salar*, postsmolts in the northern Gulf of St. Lawrence 197
MURPHY, MICHAEL L., JOHN F. THEDINGA, and K. V. KOSKI. Size and diet of juvenile Pacific salmon during seaward migration through a small estuary in southeastern Alaska 213
BOLZ, GEORGE R., and R. GREGORY LOUGH. Growth through the first six months of Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, based on daily otolith increments 223
NYMAN, ROBERT M., and DAVID G. CONOVER. The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York 237
JAHN, A. E., D. M. GADOMSKI, and M. L. SOWBY. On the role of food-seeking in the suprabenthic habit of larval white croaker, *Genyonemus lineatus* (Pisces: Sciaenidae) 251
WILLIAMS, AUSTIN B. New marine decapod crustaceans from waters influenced by hydrothermal discharge, brine, and hydrocarbon seepage 263
MARTIN, JOEL W., FRANK M. TRUESDALE, and DARRYL L. FELDER. The megalopa stage of the Gulf stone crab, *Menippe adina* Williams and Felder, 1988, with comparison of megalopae in the genus *Menippe* 289
EHRENKER, JONATHAN M. Oceanographic associations of nearshore larval and juvenile fishes and Dungeness crab megalopae off Oregon 299
DAGG, M. J., P. B. ORTNER, and J. AL-YAMANI. Winter-time distribution and abundance of copepod nauplii in the northern Gulf of Mexico 319
HERRNKIND, WILLIAM F., MARK J. BUTLER IV, and RICHARD A. TANKERSLEY. The effects of siltation on recruitment of spiny lobsters, *Panulirus argus* 331
KIRKLEY, JAMES E., and DALE E. SQUIRES. A limited information approach for determining capital stock and investment in a fishery 339
POLACHECK, TOM. Analyses of the relationship between the distribution of searching effort, tuna catches, and dolphin sightings within individual purse seine cruises 351

(Continued on back cover)

Seattle, Washington

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Fishery Bulletin

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Fishery Bulletin

CONTENTS

Vol. 86, No. 2 April 1988

PEARCY, WILLIAM G., and JOSEPH P. FISHER. Migrations of coho salmon, *Oncorhynchus kisutch*, during their first summer in the ocean 173
DUTIL, J.-D. and J.-M. COUTU. Early marine life of Atlantic salmon, *Salmo salar*, postsmolts in the northern Gulf of St. Lawrence 197
MURPHY, MICHAEL L., JOHN F. THEDINGA, and K V. KOSKI. Size and diet of juvenile Pacific salmon during seaward migration through a small estuary in southeastern Alaska 213
BOLZ, GEORGE R., and R. GREGORY LOUGH. Growth through the first six months of Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, based on daily otolith increments 223
NYMAN, ROBERT M., and DAVID O. CONOVER. The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York 237
JAHN, A. E., D. M. GADOMSKI, and M. L. SOWBY. On the role of food-seeking in the suprabenthic habit of larval white croaker, *Genyonemus lineatus* (Pisces: Sciaenidae) 251
WILLIAMS, AUSTIN B. New marine decapod crustaceans from waters influenced by hydrothermal discharge, brine, and hydrocarbon seepage 263
MARTIN, JOEL W., FRANK M. TRUESDALE, and DARRYL L. FELDER. The megalopa stage of the Gulf stone crab, *Menippe adina* Williams and Felder, 1986, with comparison of megalopae in the genus *Menippe* 289
SHENKER, JONATHAN M. Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopae off Oregon 299
DAGG, M. J., P. B. ORTNER, and J. AL-YAMANI. Winter-time distribution and abundance of copepod nauplii in the northern Gulf of Mexico 319
HERRNKIND, WILLIAM F., MARK J. BUTLER IV, and RICHARD A. TANKERSLEY. The effects of siltation on recruitment of spiny lobsters, *Panulirus argus* 331
KIRKLEY, JAMES E., and DALE E. SQUIRES. A limited information approach for determining capital stock and investment in a fishery 339
POLACHECK, TOM. Analyses of the relationship between the distribution of searching effort, tuna catches, and dolphin sightings within individual purse seine cruises 351

(Continued on next page)

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WATSON, CHERYL, ROBERT E. BOURKE, and RICHARD W. BRILL. A comprehensive theory on the etiology of burnt tuna 367
BROWN-PETERSON, NANCY, PETER THOMAS, and CONNIE R. ARNOLD. Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in South Texas 373

Notes

CHEN, CHE-TSUNG, TZYH-CHANG LEU, and SHOOU-JENG JOUNG. Notes on reproduction in the scalloped hammerhead, *Sphyrna lewini*, in northeastern Taiwan waters 389
COLLINS, MARK R., and CHARLES A. WENNER. Occurrence of young-of-the-year king *Scomberomorus cavalla*, and Spanish, *S. maculatus*, materials in commercial-type shrimp trawls along the Atlantic coast of the southeast United States 394
DEW, C. BRAXTON. Stomach contents of commercially caught Hudson River striped bass, *Morone saxatilis*, 1973–1975 397
VERNET, MARIA, JOHN R. HUNTER, and RUSSELL D. VETTER. Accumulation of age pigments (lipofuscin) in two cold-water fishes 401
MULLIN, M. M., and E. R. BROOKS. Extractable lipofuscin in larval marine fish 407
Notices: NOAA Technical Reports published during the last 6 months of 1987 ... 416

The National Marine Fisheries Service (NMFS) does not approve, recommend or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

MIGRATIONS OF COHO SALMON, *ONCORHYNCHUS KISUTCH*, DURING THEIR FIRST SUMMER IN THE OCEAN

WILLIAM G. PEARCY AND JOSEPH P. FISHER[1]

ABSTRACT

Marked juvenile coho salmon caught in fine-meshed purse seines during the summers of 1981–84 off Oregon and Washington generally demonstrated northward migrations from their rivers of ocean entrance. Northward movements in summer were preceded by southerly movements during spring, probably caused by southerly advection. Catch rates and sizes of fish caught in different months and regions of the coast also indicated northerly movements of both yearling and subyearling coho salmon. Despite this movement, the average catch of juvenile coho salmon per purse seine set along the coasts of Washington and Oregon in late summer, including marked fish from the Columbia River, was still a substantial proportion of that in May and June soon after ocean entrance, suggesting that many coho did not migrate great distances. Additionally, recoveries of marked juvenile coho salmon by sports and commercial fishermen from Alaska to California and by scientists in Alaska were generally in the region of release. These data indicate that migrations of juvenile coho are of limited extent during their first summer in the ocean and are not strong support for an earlier conclusion that juvenile coho salmon from the Columbia River, Oregon, and California may form a large proportion of the stocks of this species that migrate northward along the coastal belt in Canadian and Alaskan waters each summer.

Although there has been little research on juvenile salmon during their first summer at sea, this phase of the life history may be critical to survival and recruitment to fisheries (Hartt 1980). Highest ocean mortality is thought to occur early in marine life (Foerster 1968; Parker 1968; Ricker 1976). Production (catch and escapement) of adult coho salmon, *Oncorhynchus kisutch*, in the Oregon Production Index (OPI) Area (from Leadbetter Point, WA, to Monterey Bay, CA) is usually accurately predicted in one year by the number of precocious males (jacks) returning to index streams in the previous year (Gunsolus 1978; Oregon Department of Fish and Wildlife 1982; Pacific Fishery Management Council 1986). Hence survival from jacks to adults is fairly constant from year to year. Because survival rates from smolt to adult are variable (Nickelson 1986), however, variable year-class survival must occur before the time that jacks return, after only a few months in the ocean. This relationship, and the positive correlation between coastal upwelling and survival of OPI coho salmon (Gunsolus 1978; Scarnecchia 1981; Nickelson 1986), strongly suggest that the first few months in the ocean constitute the "critical period" in determining subsequent adult survival.

Between 1976 and 1985 the production of coho salmon in the OPI area drastically declined, despite large increases in the number of public and private smolt releases (Oregon Department of Fish and Wildlife 1982; Nickelson 1986). Reduced upwelling and ocean productivity, perhaps coupled with density-dependent mortality, is one of the hypothesized causes for this decrease in survival (Scarnecchia 1981; Peterman and Routledge 1981; McCarl and Rettig 1983; McGie 1984; Nickelson 1986). To understand the mechanisms affecting survival of juvenile salmonids at sea, we must first know where salmon reside at the time of their high and variable mortality. Are the smolts highly migratory, immediately leaving local coastal waters and migrating into waters of the Gulf of Alaska (Hartt and Dell 1986), or are they nonmigratory, spending their early ocean life in local coastal waters?

This paper summarizes research on the movements and migrations of coho salmon during their first summer in the ocean in the northeastern Pacific Ocean based on purse seine catches made mainly in coastal waters off Oregon and Washington. A few records of migrations of tagged juvenile (age .0)[2] coho salmon were given by God-

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[2]The numeral preceding and following the decimal indicate the number of winters spent in fresh water and in the ocean, respectively.

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frey (1965) and French et al. (1975), but by far the most comprehensive data were provided by Hartt (1980) and Hartt and Dell (1986). All of these studies, however, were based on recovery of mature or maturing coho in the year following tagging and on tagging in northern waters from the Strait of Juan de Fuca to the Alaska Peninsula. The only other studies of juvenile salmon in the ocean off Washington and Oregon have been restricted to within 24 km of the Columbia River (Dawley et al. 1981) or to coastal waters during 1980 (Miller et al. 1983). Our 1979–85 research, covering large areas along the coast, provides extensive and unique data on the movements of juvenile coho salmon during their first summer in the ocean.

METHODS

Purse seines, our primary sampling method, were used to sample juvenile salmonids during 1979–85 (Table 1). Cruises were in coastal waters off Oregon in 1979–80, off Oregon and southern Washington in 1981, and off Oregon and the entire Washington coast during the summers of 1982–85 (Fig. 1). During July 1984, sets were also made from northern California (lat. 40°32′N) to northern Vancouver Island (50°26′N). Except for the exploratory cruises off Oregon in 1979 and 1980, purse seine sets were usually made along east-west transect lines (Fig. 1). Sets started at the 37 m (20-fathom) contour, and continued at 9.3 km (5-mi) intervals farther offshore, usually until no salmonids were captured. Repeat sets were sometimes made when fish with missing adipose fins were common, indicating the presence of coded wire tagged (CWT) fish. In 1985, special sets were made in the vicinity of the Columbia River plume. Detailed sampling data are provided in Pearcy (1984) and our cruise reports (Wakefield et al. 1981; Fisher et al. 1982, 1983; Fisher and Pearcy 1984, 1985).

The mesh size of the seines were the same during all years, 32 mm (stretch), with 32 mm or smaller mesh in the bunts of the seines. The seine was 495 m long except in 1981 (457 m). Depths that seines fished, sometimes measured with a depth gauge on the lead line, varied among years from about 20 m to 65 m (Table 1).

Generally, purse seine sets were "round hauls", where the seiner and the skiff made a circle with the net. The seine was fully pursed after about one-half its length was aboard (half-purse sets). All sets were "blind". We attempted to use sonar on some cruises to locate concentrations of salmonids but were unsuccessful. Radar was sometimes used to determine the distance between the seiner and the skiff when a semicircle was made with the net. Each round haul encompassed about 17,000 m^2 (1981) or 19,000 m^2 (1979–85). To determine the direction of movement of fish, eight "half-round" hauls, or "semicircular" sets, were made in 1979, where the entire net formed an open semicircle. Paired sets were made in close succession, with sets open in a northern and a southern direction, at four locations. The seine was open for the same duration (15–45 minutes, depending on location) in each paired set while

TABLE 1.—Summary of number of purse seine sets and latitudinal range of sampling, 1979–85.

Year	Dates of cruises	No. of sets[1]	Latitudinal range of sampling		Purse seine Length (m)	Purse seine Depth (m)
1979	18–29 June	56	Cape Disappointment to Cape Arago	46°20′–43°18′	495	20
1980	20–28 June	36	Cape Disappointment to Alsea River	46°20′–44°30′	495	20
1981	16–25 May	63	Willapa Bay to Alsea River	46°35′–44°25′	495	20
	9–18 June	67	Willapa Bay to Cut Creek	46°35′–43°11′	495	20
	9–19 July	67	Willapa Bay to Alsea River	46°35′–44°25′	457	49
	8–19 Aug.	66	Willapa Bay to Cut Creek	46°36′–44°11′	457	49
1982	19 May–2 June	62	Waatch Point to Siuslaw River	48°21′–44°00′	495	[2]65
	7–22 June	57	Quinault River to Yachats	47°21′–44°20′	495	[2]65
	4–14 Sept.	42	Quinault River to Yachats	47°20′–44°19′	495	[2]65
1983	16–27 May	56	Waatch Point to Yachats	48°21′–44°20′	495	[2]49
	9–27 June	58	Waatch Point to Four Mile Creek	48°20′–43°00′	495	[2]49
	15–24 Sept.	53	Waatch Point to Coos Bay	48°20′–43°28′	495	[2]49
1984	4–20 June	69	Waatch Point to Coos Bay	48°20′–43°27′	495	[2]49
	9 July–3 Aug.	65	Winter Harbor, B.C. to False Cape, CA	50°26′–40°32′	495	[2]49
	1–15 Sept.	63	Waatch Point to Siuslaw River	48°20′–44°00′	495	[2]49
1985	29 May–25 June	112	Sea Lion Rock to Coos Bay	48°00′–43°27′	495	[2]25

[1]Quantitative sets.
[2]Measured with depth guage.

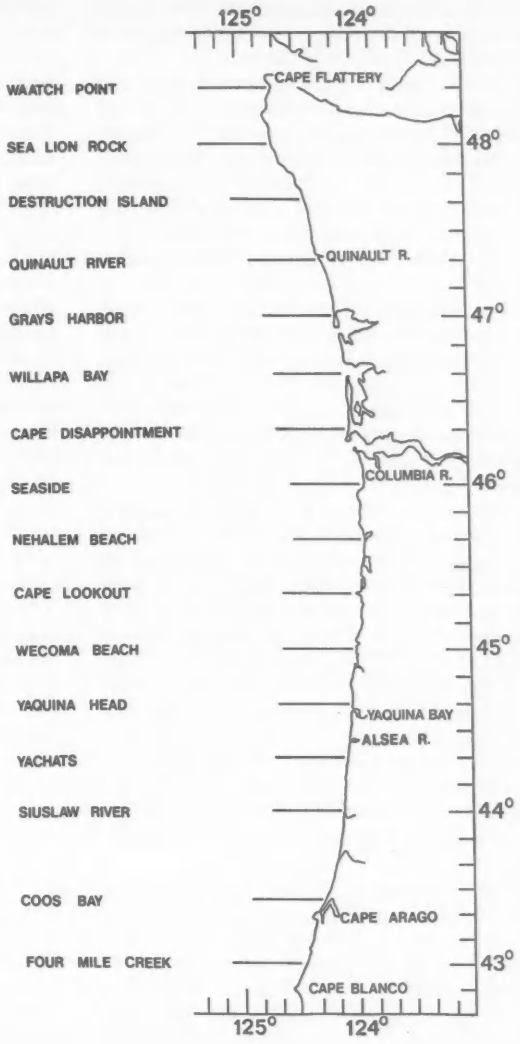

FIGURE 1.—Locations of purse seine transects off the Oregon and Washington coasts.

the vessel and skiff towed the seine only fast enough to maintain a constant net opening.

The purse seine catches were either dip-netted from the bunt of the seine while it was alongside the vessel, brailed aboard, or hauled aboard in the bunt, depending on the composition and size of the catch.

In 1979 and 1980, juvenile salmon preserved in formalin were identified ashore. In 1981–85, juvenile salmon were identified to species at sea, fork length (FL) was measured to the nearest millimeter and then they were individually wrapped in labelled plastic bags and frozen. All salmonids with marks or missing adipose fins were frozen. When large numbers of juvenile salmonids were caught in a set, most unmarked fish were released after they were measured.

In order to increase the numbers of marked fish released into our study area we marked about 1.5 million coho smolts in 1981 and 835,000 in 1982 using fluorescent pigment propelled by compressed air (see Phinney et al. 1967) prior to their

transport from Oregon Aqua-Foods, Inc. (OAF) hatchery to their ocean release facilities at Yaquina Bay or Coos Bay, OR.

In the laboratory ashore, species identifications were confirmed and individuals remeasured and reexamined for both fluorescent marks (under ultraviolet light 1981–82) and missing adipose fins or other marks (1979–85). Coded-wire tags from the heads of salmonids with missing adipose fins were decoded by personnel from the Oregon Department of Fish and Wildlife, Clackamas Laboratory.

Juvenile or age .0 (first year in the ocean) coho salmon were distinguished from adult or age .1 (second year in the ocean) coho salmon by examination of size-frequency histograms and scales. The division between age .0 and .1 coho progressed from approximately 300 to 420 mm FL from May to September, in most years. Most coho salmon migrated to the ocean a little over one year after hatching (age 1.0), but OAF released large numbers of subyearling (age 0.0) smolts into Yaquina Bay and Coos Bay. These two age groups of smolts were distinguished by the radial distance to the 21st circulus on scales removed from the preferred area (Clutter and Whitesel 1956) of the fish. The accuracy of this method for distinguishing known age 0.0 and 1.0 fish was approximately 85–90%. In the years 1981–85, scales from 52% of the 4,222 juvenile coho sampled were analyzed. The estimated numbers of age 0.0 and 1.0 fish represented in different geographic areas and cruises were then extrapolated from their proportions in each 10 mm length interval.

Distances traveled and movement rates were estimated from actual distances between sites of release and entry into the ocean, and from straight-line distances between ocean entry and recapture locations for CWT or fluorescent marked juvenile coho salmon that were recovered in the ocean within 10 days of release. These distances and swimming speeds are minimal estimates.

In addition to purse seining, fine-meshed monofilament gill nets were used off the Oregon coast (ca. lat. 45°00'N, long. 124°21'W) during 24 and 25 July 1985, from the training vessel *Oshoro Maru*, to determine depth and direction of swimming of juvenile salmonids. Surface and subsurface nets were used. The surface gill nets were 2,050 m long, and fished from depths of 0–6 m with 11 mesh sizes ranging from 29 to 121 mm (stretch). The subsurface nets were 500 m long and consisted of four mesh sizes ranging from 29 to 42 mm; they were suspended below large (300–400 mm) mesh to fish at depths of 5–12 m. Four sets were made in an east-west direction with soak-times of about 4–9 hours. As the gill nets were hauled, the direction that each juvenile salmonid was heading when caught, and its depth in the net (upper, middle, or lower section) were noted. Each juvenile salmonid was given a consecutive number and frozen for later identification. Comparisons of catch rates in the surface and subsurface nets were based on equal lengths of the four mesh sizes of the subsurface net, standardized to 10 hours of fishing time.

Information on the location of landings of marked juvenile coho by commercial and sports fishermen was provided by the Pacific Marine Fisheries Commission (PMFC), (PMFC 1980, 1981, 1984a, b, c, 1985a, b), from lists of nonstandard recoveries (Johnson PMFC unpubl. data), and from state agencies. The actual numbers of tagged fish, and the total numbers of tagged fish estimated from the proportions of the catch sampled are reported.

To determine if juvenile coho salmon were sexually precocious "jacks", we examined testes from 542 juvenile males caught in July 1981 and 1984, in August 1981, and in September 1982, 1983, and 1984. All developed and some undeveloped testes (ribbonlike, with no thickening), as determined by visual inspection, were weighed (123) and gonadal-somatic indices (GSI = testes wt./body wt. × 100) were determined.

RESULTS AND DISCUSSION

Swimming Direction

Of the 106 juvenile coho salmon captured during June in paired, half-round purse seine sets, all but two were in the sets open to the south (Table 2). This suggests that juvenile coho salmon

TABLE 2.—Catches of coho salmon in semicircular purse seine sets open to the south (S) and north (N) off Oregon, June 1979.

		Age .0		Age .1	
Location	Km offshore	S	N	S	N
Clatsop Spit	12.6	57	0	2	6
Clatsop Spit	18.5	37	0	15	37
Clatsop Spit	18.5	7	0	6	8
Newport	9.4	3	2	0	9
		98%	2%	28%	72%

were swimming to the north during this sampling period. Maturing fish over 300 mm FL (age .1 coho) showed the opposite trend.

Miller et al. (1983) made several hundred paired purse seine sets open to the south and north during three cruises off the northern Oregon-southern Washington coasts in 1980. During their May-June cruise, they caught 76% of the juvenile coho salmon, 80% of the chinook salmon, and almost all the steelhead trout in sets open to the south, indicating northward movement. We note a positive relation between the proportion of juvenile salmon caught in south-facing sets in their three cruises and strength of upwelling during these cruises (mean daily Bakun indices of 52, 39, and 19 $m^3\ s^{-1}\ 100\ m^{-1}$ coastline at 45°N, 125°W in May, July, and August, respectively (Mason and Bakun 1986)), suggesting that surface currents to the south resulting from Ekman transport may be cues for orientation of salmon smolts.

Hartt (1980) and Hartt and Dell (1986) found that 83% of the combined species of juvenile salmonids caught in 19 paired purse sets along the coast from Cape Flattery, WA to Yakutat, AK were caught in sets held open to the southeast and only 17% in sets open to the northwest and north. They concluded that juvenile salmonids tended to migrate in a northwest direction along the coast during July–September.

Of the 100 juvenile coho salmon (135–315 mm FL) caught in the gill nets set in an east-west direction off the Oregon coast in July 1985, 90 coho were caught as they approached the southern face of the gill net (heading north) and 10 in the northern face (heading south). Jaenicke et al. (1984) reported that 63% of the juvenile coho caught in a surface gill net fished off southeastern Alaska in July moved north at night, but only 6% moved to the north during the day.

Available data indicate that most juvenile coho salmon caught off Oregon and southern Washington, as well as juveniles farther to the north, are predominantely swimming in a northerly direction during summer months.

Depth Distribution

One-half of the juvenile coho salmon caught in gill nets set off the Oregon Coast in 1985 were in the upper 2 m of the surface gill net (Table 3). Catches in the surface net exceeded those in the subsurface net, except for the last set that fished during daylight hours, indicating that juvenile coho salmon were most common in the upper 4 m of the water column.

Other information on the vertical distribution of maturing coho and other species of salmon caught in gill nets or with longlines in oceanic waters also indicates that they usually swim near the surface, between 0 and 20 m (Manzer 1964; Godfrey 1965; Godfrey et al. 1975). Machidori (1966), for example, fished gill nets from the surface to 50 m and caught 79% of the coho salmon in the upper 10 m of the gill net. Although catches in gill nets at different depths may be biased by vertical differences in avoidance reactions to the net or swimming speeds (Hartt 1975), acoustical methods have also shown that salmon are usually distributed near the surface (Susuki and Sonoda 1972; Lord et al. 1976). We conclude that most juvenile coho salmon in coastal waters and maturing coho in oceanic waters reside at depths above 20 m, the minimum depth that our purse seine fished. We recognize, however, that maturing coho and other species of salmon may feed in deeper water. Some salmon (including coho salmon) caught in surface gill nets in the oceanic waters of the Gulf of Alaska contained prey in their stomachs characteristic of mesopelagic depths (200–1,000 m), suggesting that some individuals may feed well below the thermocline (Pearcy et al. in press).

TABLE 3.—Catches of juvenile coho salmon in four gill net sets in 50 m lengths of 29, 33, 37, and 42 mm mesh at different depths and times 24–25 July 1985, each set adjusted to 10-h fishing duration.

	Depth in meters					
	Surface net			Subsurface net		
Times of set	0–2	2–4	4–6	5–7	7–9	9–12
0913–1702	2.5	3.8	0	1.3	1.3	0
2001–0104	25.0	11.5	0	0	0	1.9
0248–0701	42.8	2.4	2.4	9.5	16.6	0
0830–1737	1.1	0	0	6.6	7.7	5.5
Total catch	51	16	1	11	15	6
Percent of total catch	50.3	12.5	1.7	12.3	18.0	5.2

North-South Trends in Catch per Set and Sizes of Juvenile Coho

Variations in the average catches and sizes of juvenile coho salmon in purse seine sets in different regions of the Oregon-Washington coast during the summer provide indirect evidence for north-south coastal movements. Histograms showing average catches per set for 10 mm size

groups of juvenile coho, classified as age 0.0 or 1.0 from scale analysis, are shown in Figure 2, for 1981–84 in three regions: (A) Cape Flattery, WA to Grays Harbor, WA (called Washington), (B) Willapa Bay, WA to Nehalem Bay, OR (Columbia River region), and (C) Cape Lookout, OR to Coos Bay, OR (Oregon) (Fig. 1). In May of 1981, 1982, and 1983, average catch per set of yearling (age 1.0) coho generally decreased from the southern to the northern regions. Catches were highest off Oregon (Area C) or the Columbia River (Area B) and lowest off Washington (Area A) in May of 1982 and 1983. This trend was reversed later in the summer. In June of 1981, 1983, and 1984, lowest catches were found in the Oregon region. By August or September 1981–84, highest catches consistently occurred off the Columbia River or Washington and few yearling fish were caught off Oregon. These shifts in abundance suggest a northerly movement of age 1.0 smolts during the summer. Highest catch rates occurred in May and June of 1981 and 1982 when an average of over 10 juvenile coho salmon were caught in most sets.

Subyearling or age 0.0 coho salmon released from private facilities at Yaquina and Coos Bays provide more direct evidence on movements. Subyearling coho salmon clearly demonstrated northward dispersal. They were most common in our catches of July 1981 and September 1982, 1983, and 1984 (Fig. 2). They were apparently more numerous than age 1.0 coho salmon in the Oregon region during June–August 1981 and September 1982, and in the Oregon and Columbia River regions in September 1983. The catches and proportions of age 0.0 coho salmon increased off Oregon during the summer because they were released from hatcheries later in the summer than yearling coho salmon. They were found in the most northern region sampled late in the

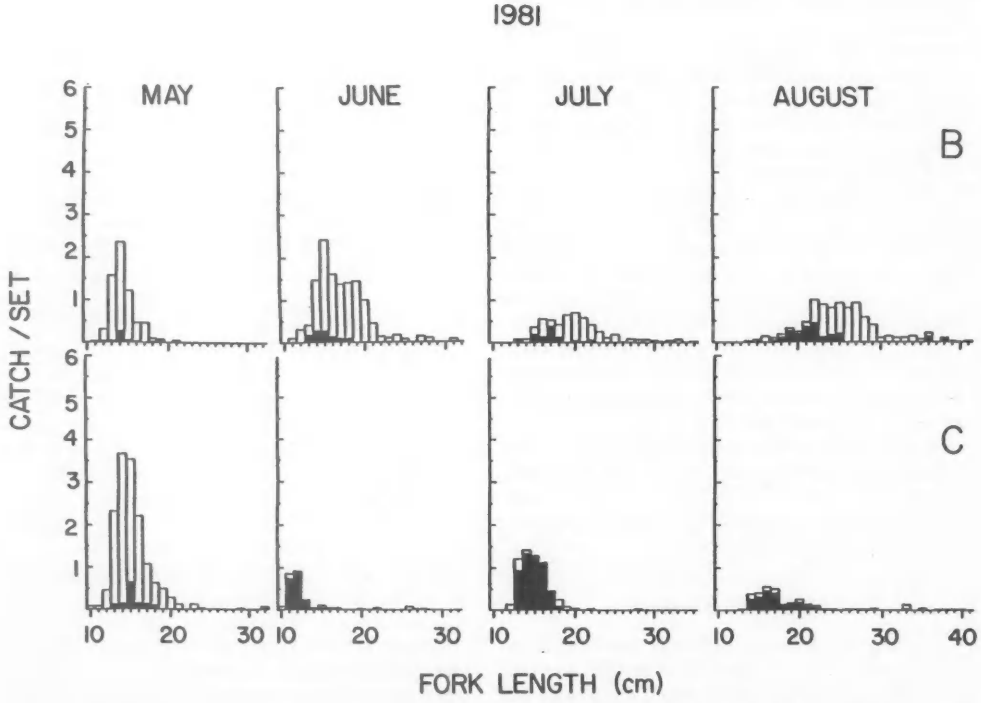

FIGURE 2.—Catch per purse seine set of age 1.0 (open) and age 0.0 (shaded) juvenile coho by 10 mm length groups during different months, 1981–84, for three regions of the Oregon-Washington coast: (A) Cape Flattery to Grays Harbor, WA, (B) Willapa Bay, WA to Nehalem Beach, OR, (C) Cape Lookout to California.

summer of all years. Their abundance, as that of age 1.0 coho salmon, also increased during the summer off Washington where they intermingled with age 1.0 coho salmon. Because the Oregon region included the release locations of all age 0.0 coho salmon, our figures provide no information on southward movements of these fish.

The mean lengths of both age 0.0 and 1.0 coho salmon increased from the southern to the northern areas during most months. Larger age 0.0 and 1.0 coho salmon were caught off Washington than Oregon during the late summer, 1981–84 (Fig. 2), providing corroborative evidence for northward migration of coho salmon. Larger, and presumably older, fish were found farther to the north than smaller fish.

Despite northward movements, many yearling coho salmon did not migrate out of the sampling area, but remained in coastal waters off Oregon and Washington during the entire summer. Mean coastwide catch per set of yearling coho salmon in August 1981 and September 1982, 1983, and 1984

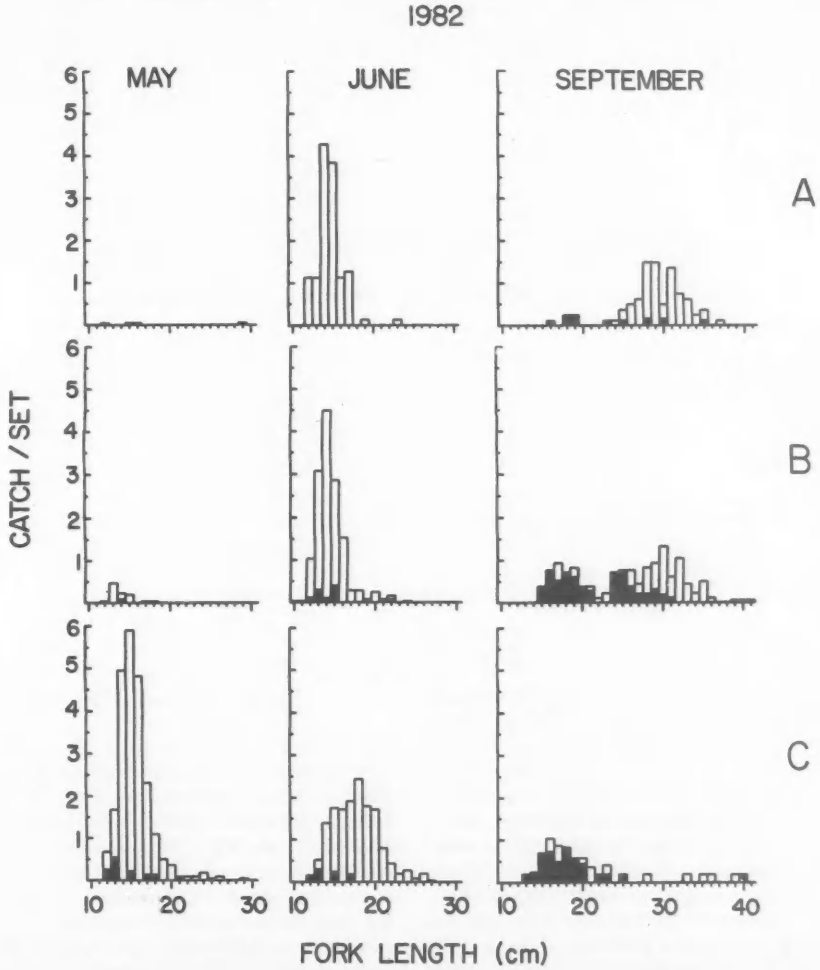

FIGURE 2.—*Continued*.

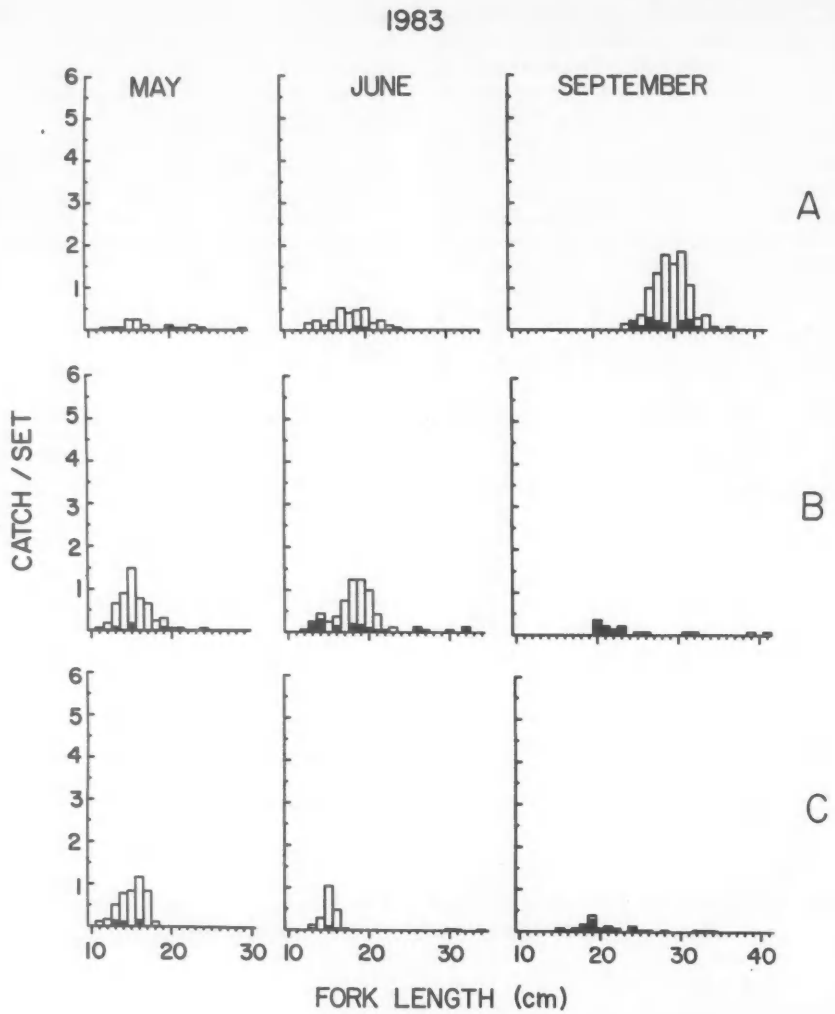

FIGURE 2.—*Continued*.

was 61%, 42%, 81%, and 77% respectively, of that in June of the same years. In September 1983, a strong El Niño year (Pearcy and Schoener 1987), almost all yearling juvenile coho salmon were caught at the extreme northern transect off Cape Flattery, but in August or September of other years they were more evenly distributed off the Columbia River and the Washington coast.

In July 1984, we sampled both north (15 sets off the west coast of Vancouver Island) and south (5 sets off northern California) of Washington and Oregon. Catches per set of yearling and subyearling juvenile coho salmon were higher off the Columbia River (5.1), the area of greatest smolt production, and off Washington (3.5) than off Vancouver Island (1.8), Oregon (1.7), and California (1.2). This shows that as late as July juvenile coho salmon occurred in coastal waters of all regions and were not concentrated off Vancouver Island or California.

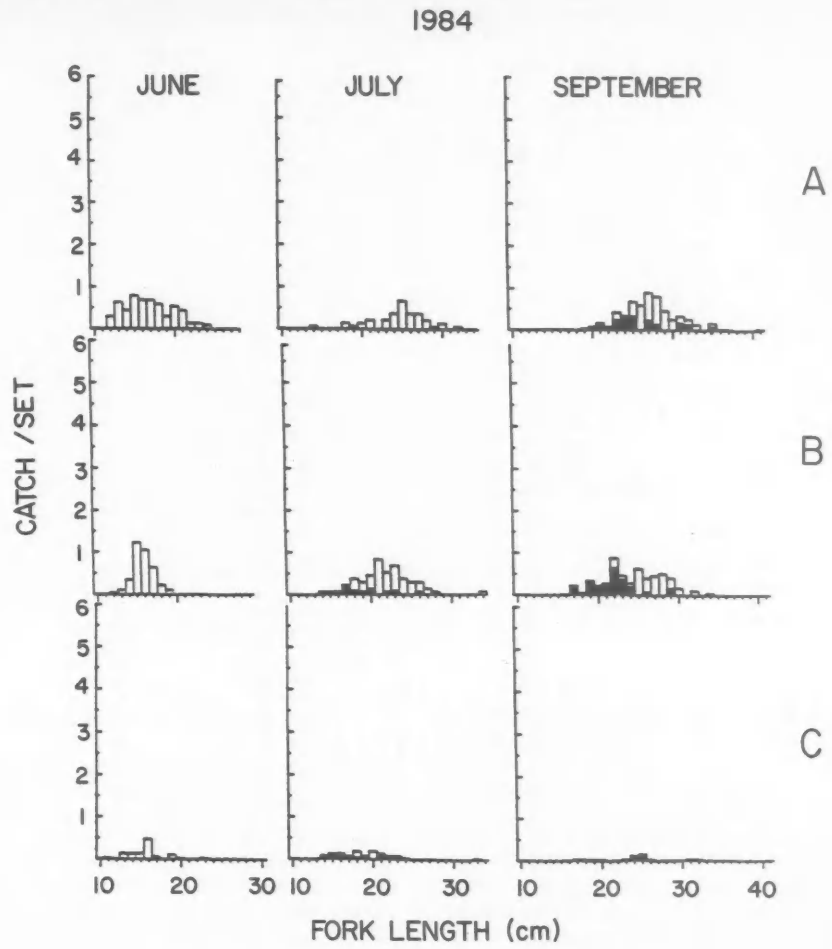

FIGURE 2.—*Continued*.

The Question of "Jacks"

Are the juvenile coho salmon off Oregon and Washington in late summer relatively nonmigratory because they are sexually precocious? GSI were almost always <0.1% for those fish visually classified as "undeveloped". GSI's from fish with "developed" testes ranged from 0.2% to 1.0% in July 1981 and 1984 in fish >250 mm FL; from 0.3% to 5.6% in August 1981, mostly in fish >280 mm FL; and from 2.4% to 6.6% (except for one value at 0.6) in September 1982, 1983, and 1984 in fish >300 mm FL (Fig. 3). In August 1981, and clearly in September 1982, 1983, and 1984, two distinct groups of fish were evident: "jacks", with developing testes (GSI >0.3% August or GSI >2.0% September), and "nonjacks", which showed no development (GSI <0.1%).

The total numbers of jacks and nonjacks in each 50 mm length group were estimated for the catch during August 1981 and September 1982, 1983, and 1984 from the ratio of jacks and nonjacks in the sample (Table 4). Only 8.4%, 4.8%, 5.2%, and 2.8% of all juvenile fish (male and female) were "jacks" in August 1981 and September 1982, 1983, and 1984, respectively. However jacks com-

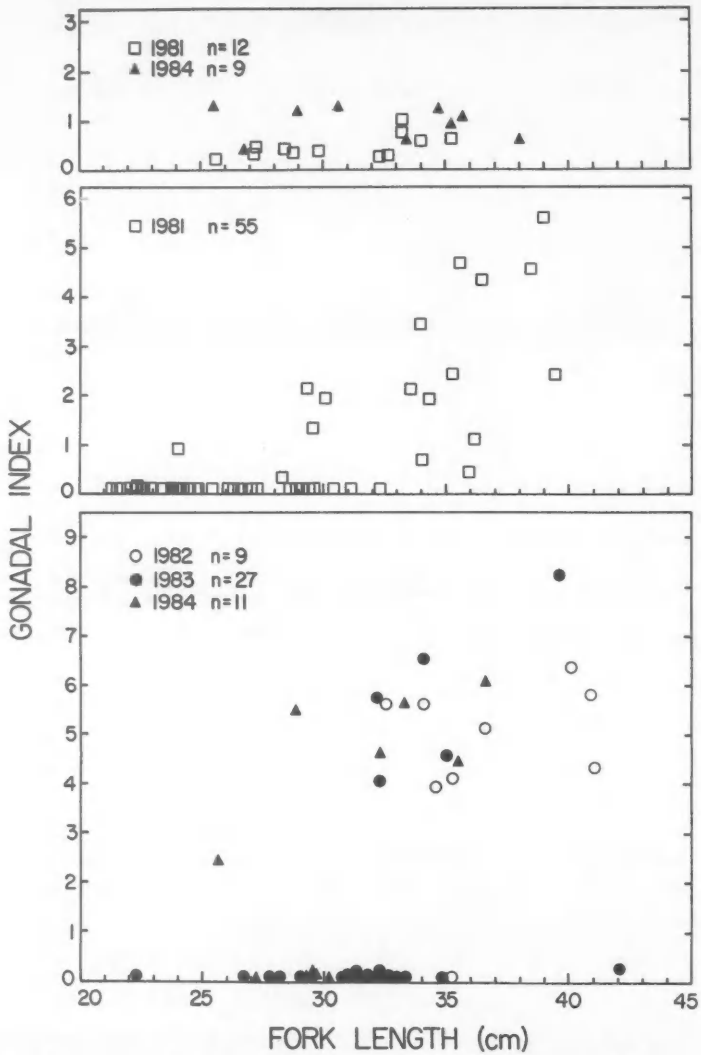

FIGURE 3.—Gonadal-somatic index (testis wt/total body wt) × 100 of juvenile coho salmon vs. length of fish for July, August, and September 1981–84. Only data for those testes actually weighed are shown.

prised a higher percentage of fish larger than 300 mm FL in August 1981 and larger than 350 mm FL in September 1982, 1983, and 1984. These results indicate that most juvenile coho salmon caught off Oregon and Washington were not sexually precocious. Thus, the relatively large catches of juvenile coho salmon in late summer are explained by lack of strong migrational tendencies of juvenile coho salmon in this region and not by a high proportion of precocious "jacks" that resided in this region as a prelude to re-entry of streams for spawning.

TABLE 4.—The percent of coho salmon jacks and males, by length groups, in the total catch, August 1981 and September 1982–84.

Date	Fork length (mm)	Number of fish examined	% males	Number of jacks[1]	Total catch	Est. total jacks	Est. % jacks of total
Aug. 1981	<200	71	60.6	0	111	0	0
	201–250	63	60.0	1	115	2	1.7
	251–300	55	47.3	4	104	8	7.7
	301–350	16	81.3	4	22	6	27.3
	351–420	10	80.0	8	19	15	78.9
	Total	215	59.5	17	371	31	8.4
Sept. 1982	<200	56	55.4	0	125	0	0
	201–250	21	76.2	0	54	0	0
	251–300	22	63.6	0	109	0	0
	301–350	33	69.7	3	97	9	9.3
	351–420	13	53.8	5	28	11	39.3
	Total	145	62.8	8	413	20	4.8
Sept. 1983	<200	16	62.5	0	18	0	0
	201–250	23	47.8	0	25	0	0
	251–300	23	56.5	0	71	0	0
	301–350	39	61.5	4	77	8	10.4
	351–420	2	0	1	3	2	66.7
	Total	103	58.3	5	194	10	5.2
Sept. 1984	<200	6	33.3	0	15	0	0
	201–250	38	47.4	0	69	0	0
	251–300	90	50.0	2	128	3	2.3
	301–350	27	55.6	12	31	2	6.5
	351–420	6	33.3	2	7	2	28.6
	Total	167	49.1	16	250	7	2.8

[1]Jack is defined as a male whose testes wt./total body wt. × 100 > 0.3% in August and >2.0% in September.

Movements of Marked Fish

Direct evidence of movements of juvenile coho salmon was obtained from capture of marked fish containing coded wire tags or marked with fluorescent pigment. The generalized pattern of movements that emerges for 1981–85 is an initial movement of most juvenile coho salmon to the south soon after ocean entry in May and June and then a reversal of movement with most fish migrating to the north by August and September (Figs. 4–8). These trends are discussed for fish originating from the Columbia River, Oregon coastal, Washington coastal, and private hatcheries.

Columbia River

Juvenile coho salmon originating from hatcheries on the Columbia River were usually recovered south of the Columbia River in May. This trend was especially obvious in May 1982 when all 22 marked fish which were recovered moved south, some as far as 175 km (Fig. 5). In May 1981, all but one of 14 marked Columbia River fish were caught to the south, three as far as 180 and 204 km (Fig. 4). In May 1983, all four fish were taken south of the mouth of the Columbia River (Fig. 6).

During June and July of all years, marked Columbia River coho salmon were recovered in nearly equal proportions both north and south of the river mouth, except in June 1982 when 15 of 17 fish were found to the south (Figs. 4–8). By September, all marked Columbia River coho salmon were captured north of the river, including fish captured off the Quinault River in September 1982 and off Cape Flattery in September 1984. Fish were also caught close to the mouth of the Columbia River in July, August, and September, indicating that some marked juvenile coho salmon did not undertake extensive migrations at sea.

In two sets on the Wecoma Beach Transect on 1 June 1982 we caught 17 marked juvenile coho salmon released between 30 April and 6 May from six hatcheries on the Columbia River. Based on downstream migration rates for these groups to Jones Beach (Dawley et al. 1985) and assuming similar rates from Jones Beach to the ocean, these fish had probably been in the ocean for <10 days before recapture. This indicates that some juve-

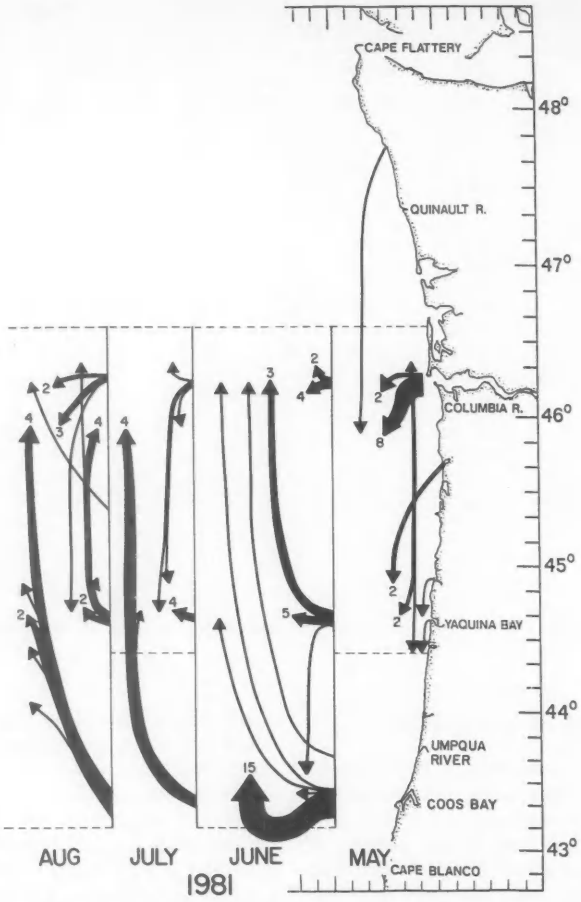

FIGURE 4.—North-south movements of marked juvenile coho salmon captured in purse seines, May–August 1981. The width of the lines are approximately proportional to the number of fish. Numbers at end of arrows indicate number of fish captured. Arrows without numbers and thin lines represent single fish. Inshore-offshore movements are not shown. Dashed lines indicate latitudinal extent of sampling.

nile coho salmon released from hatcheries at about the same time tended to stay together during their downstream migration in the Columbia River and during early residency in the ocean.

Oregon Public Coastal Hatcheries

We captured marked fish originating from public Oregon coastal hatcheries both north and south of the latitude of ocean entrance in May. A total of five fish were found to the south, while 11 fish were found to the north in May (Figs. 4–8). With the exception of one coho salmon from the Umpqua River in June 1983 and two from the Rogue River in July 1984 (Figs. 6, 7), the other 25 fish taken after May were captured north of where they entered the ocean. Northerly movements into Washington waters occurred by June 1983 and 1985 (Figs. 6, 8).

The southward movements of two juvenile coho salmon released from the Rogue River (south of Cape Blanco) and captured off northern Califor-

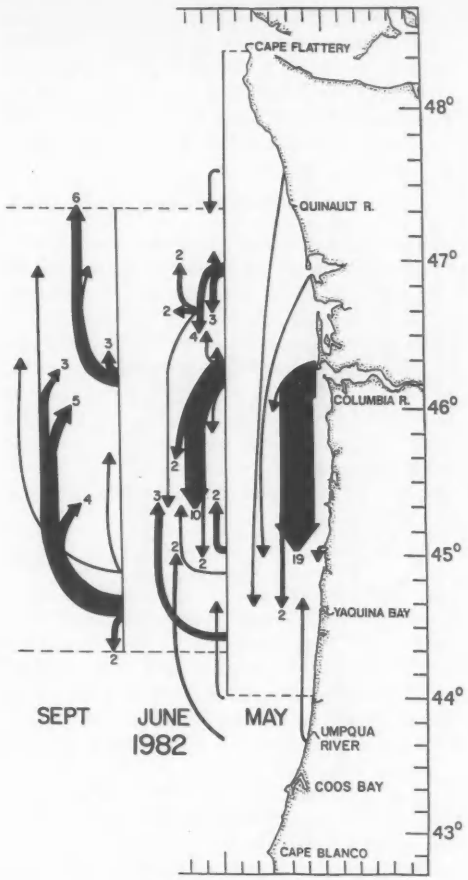

FIGURE 5.—North-south movements of marked juvenile coho salmon captured in purse seines, May, June, and September 1982. The width of the lines are approximately proportional to the number of fish. Numbers at end of arrows indicate number of fish captured. Arrows without numbers and thin lines represent single fish. Inshore-offshore movements are not shown. Dashed lines indicate latitudinal extent of sampling.

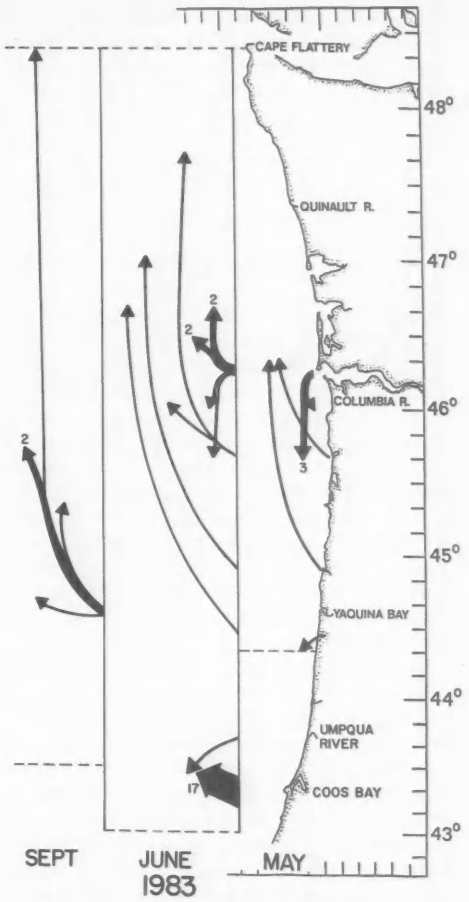

FIGURE 6.—North-south movements of marked juvenile coho salmon captured in purse seines, May, June, and September 1983. The width of the lines are approximately proportional to the number of fish. Numbers at end of arrows indicate number of fish captured. Arrows without numbers and thin lines represent single fish. Inshore-offshore movements are not shown. Dashed lines indicate latitudinal extent of sampling.

nia during July 1984 are notable (Fig. 7). They were captured in our only cruise into California waters and represent the only recoveries of marked juvenile coho salmon originating from hatcheries south of Cape Blanco in all six years of sampling. Although ocean sampling was limited south of Coos Bay, if juvenile coho salmon from southern Oregon and northern California hatcheries had migrated north of Coos Bay, we would expect them to be represented in our catches. The fact that they were not caught in this northern region, but two were caught after swimming to the south, suggests that juvenile coho salmon originating in streams south of Cape Blanco may migrate south, possibly occupying the region of intense coastal upwelling off northern California during their first summer in the ocean. The catch of over 70% of the adult coho

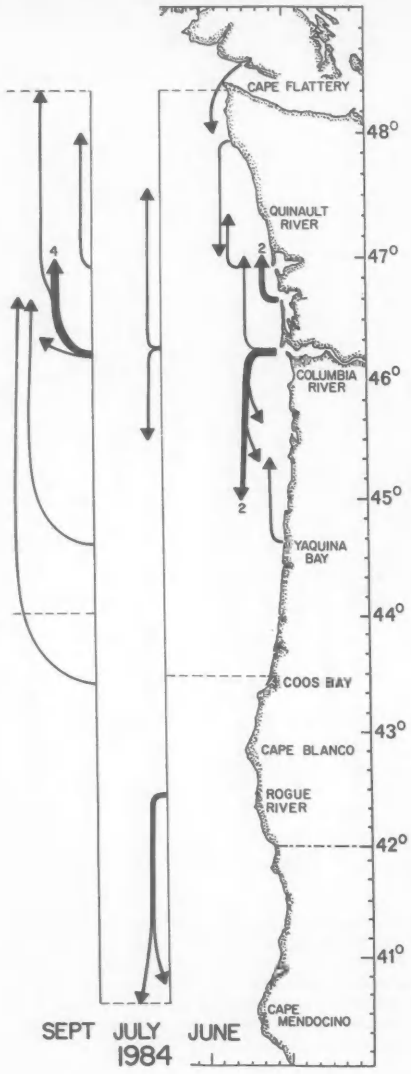

FIGURE 7.—North-south movements of marked juvenile coho salmon captured in purse seines, June–September 1984. The width of the lines are approximately proportional to the number of fish. Numbers at end of arrows indicate number of fish captured. Arrows without numbers and thin lines represent single fish. Inshore-offshore movements are not shown. Dashed lines indicate latitudinal extent of sampling.

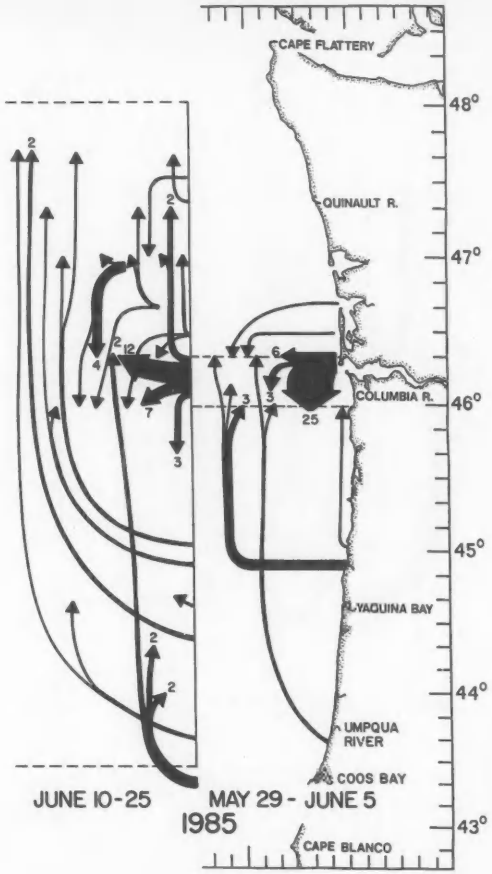

FIGURE 8.—North-south movements of marked juvenile coho salmon captured in purse seines, 29 May–5 June and 10–25 June. The width of the lines are approximately proportional to the number of fish. Numbers at end of arrows indicate number of fish captured. Arrows without numbers and thin lines represent single fish. Inshore-offshore movements are not shown. Dashed lines indicate latitudinal extent of sampling.

salmon from the Rogue River in the troll fishery off California (R. Garrison[3]) is further evidence for a southern distribution of this stock. Marked juvenile coho salmon from California hatcheries were reported from the sports fishery off southern Oregon, however, as will be shown later.

Washington Coastal Hatcheries

Juvenile coho salmon from Washington public hatcheries demonstrated southerly movements, sometimes into Oregon waters, during May 1981 and 1982 (Figs. 4, 5). During June 1982, 1984, and 1985, Washington coastal fish were found both north and south of ocean entry. Except for one fish that moved north in September 1984, no Washington coastal fish were taken in August or September of other years, suggesting that most Washington fish may have migrated out of our sampling area by late summer.

Oregon Private Hatcheries

All marked juvenile coho salmon originating from Yaquina and Coos Bays that we captured at sea were from private hatcheries. Those from Yaquina Bay were mainly age 0.0 smolts from OAF, those from Coos Bay were either age 1.0 smolts from Anadromous, Inc. or age 0.0 smolts from OAF. Forty-one recoveries of marked OAF fish released from Yaquina Bay were caught to the north while only 4 were to the south of Yaquina Bay. In general, more juvenile coho salmon from Yaquina Bay were captured in late than early summer, and distances traveled to the north were largest (up to 413 km) for fish caught in later summer (Figs. 4–8). All recoveries of marked Anadromous, Inc. and OAF fish released into Coos Bay were to the north in all years. Large northerly movements were demonstrated by some of these fish (Figs. 4, 6, 8). Since our sampling in the ocean usually did not extend south of Coos Bay, recoveries of these fish are biased to the north; however, strong northward movements of these stocks were indicated.

Rates of Movement

Recoveries of marked juvenile coho salmon in the ocean provided information on the minimum rates of movement from hatchery release to capture in the ocean. Some fish moved rapidly through estuaries into the ocean. We captured some tag-groups in the ocean only a few days after the median date of capture at Jones Beach (75 km from the ocean) as reported by Dawley et al. (1985): 5 fish after 2 days in 1981, 6 fish after 3–11 days in 1981, 8 fish after 1–14 days in 1982, and 5 fish after 3–8 days in 1983. Dawley et al. (1986) found average rates of movement of 14–23 km d^{-1} for marked groups of coho smolts from areas of release on the Columbia River to river km 75, and rates of movement that were 40% faster from river km 75 to the lower Columbia River estuary and to the ocean plume. These recoveries and those reported by Miller et al. (1983) for yearling chinook salmon and steelhead trout indicate rapid movements of juvenile salmonids of over 20 km d^{-1} through the Columbia River estuary.

Some juvenile coho salmon released from Yaquina Bay and Coos Bay also demonstrated rapid movements into and in the ocean, e.g., 17 Anadromous, Inc. fish were captured 11 km north of Coos Bay only two days after release in June 1983 (Table 5). Myers (1980) described an exponential decrease in the catches of juvenile coho salmon released from the OAF facility into Yaquina Bay; about one-half the fish from marked groups remaining in the bay after 1.7–9.0 days. Juvenile coho salmon apparently emigrate rapidly from estuaries into the ocean.

Some of the marked fish recovered within 10 days of release demonstrated rapid movements down-rivers or in the ocean. Twenty-four fish traversed 10 km d^{-1} or more largely in the ocean, in both north and south directions (Table 5). Four fish released in bays or in the ocean moved over 18.8 km d^{-1}. Two of these swam to the north, presumably against coastal currents. These speeds are equivalent to 1.7 body lengths (BL) per second or more and suggest that some fish must be traveling nearly straight courses during 24-h days, since 1–3 BL s^{-1} are thought to be optimal cruising speeds for small (<20 cm) pelagic fishes (Weihs 1973; Ware 1978). These maximum rates of movement for purse seine caught juvenile coho salmon are similar to those estimated by Hartt (1980) and Hartt and Dell (1986) for tagged sockeye salmon during their first summer in the ocean: 14–27 km d^{-1} for 11 Fraser River fish and 6–14 km d^{-1} for 10 Skeena River fish that were between about 8 and 23 cm in length during the migration period.

[3]R. Garrison, Oregon Department of Fish and Wildlife, Corvallis, OR 97330, pers. commun. December 1983.

TABLE 5.—Release information and mean travel speeds in kilometers per day and body length (BL) per second for CWT and fluorescent-pigment marked age .0 coho salmon recovered in the ocean within 10 days of release. CR = Columbia River; OAF = Oregon Aqua Foods, Inc., (OAF Yaquina is 3.7 km from ocean; OAF Coos is 14 km from the ocean), Anad. = Anadromous Inc. (7.4 km from the ocean).

Year	No.	Release location	Date released	Median days to recovery	Mean FL	Mean km/d	Mean BL/s	Direction of movement
1981	1	Big Cr. (CR)	8 June	3	153	22.2	1.7	S
	1	Tanner Cr. (CR)	6 July	6	138	41.0	3.4	N
	1	OAF Yaquina	11 May	7	140	4.0	0.3	S
	1	OAF Yaquina	12 June	2	124	14.5	1.4	N
	2	Anad. Coos	8 June	9	179	2.3	0.2	N
	2	OAF Yaquina	10–15 June	2	124	3.7	0.3	N
	1	OAF Yaquina	10–15 June	2	123	10.2	1.0	N
	1	OAF Yaquina	10–15 June	2	126	18.8	1.7	N
	11	OAF Coos	5–9 June	10	122	1.9	0.2	N
	1	OAF Yaquina	10–15 June	5	124	24.0	2.2	S
	1	OAF Coos	5–9 June	7	136	20.1	1.7	N
1983	17	Anad. Coos	26 June	2	156	11.2	0.8	N
1984	1	OAF-Offshore	7 June	7	143	11.3	0.9	N
1985	6	Tongue Pt. (CR)	24 May	6	151	9.5	0.7	S
	1	Offshore-22 km	30 May	0.9	134	22.0	1.9	S
	1	Naselle River	20 May	9	143	7.8	0.6	S
	1	Cowlitz River	31 May–6 June	2.5	144	88.0	7.1	N

Effects of Ocean Currents

The tendency for juvenile coho salmon to move to the south early in the summer and to the north later in the summer (Figs. 4–8) may be related to advection of water and the size, orientation, and swimming speeds of fish. Generally, surface currents are to the south off Oregon and Washington in the early summer owing to prevailing northwesterly winds (Hickey 1979; Huyer 1983). Southward flow averaging 17–34 km d^{-1} (Huyer et al. 1975, 1979) has been measured near the surface. May and June are periods of peak outflow of the Columbia River, so fish entering the ocean at this time, especially in the Columbia River plume, may be displaced to the south by advection of surface waters. Southward flow is at a maximum in the coastal jet which is strongest (~22 km d^{-1}) during the spring about 15–20 km from shore (Kundu and Allen 1976; Huyer et al. 1979). Since currents can be equivalent to 1.7 BL s^{-1} for a 15 cm smolt, advection alone could explain the southward movement of most marked Columbia River fish during May and June but not the rapid northward movement of fish during this period (see Figures 4–7).

Coastal Oregon fish were often found to the north in May and June, but these fish were usually substantially larger and generally released much earlier in the spring than Columbia River fish, and were presumably better able to swim against the current. Later in the summer when Columbia River hatchery fish had grown larger, movement was also predominately northward. In August and September southward velocities of surface coastal currents are diminished and the mean may be near zero (Huyer et al. 1975). Northward movements during the summer off Oregon and Washington generally cannot be explained by passive drift and in most years must entail active, oriented swimming.

The northern El Niño of 1982–83, which had severe effects on the growth and survival of adult and jack coho salmon (Pearcy et al. 1985; Johnson 1984; Pearcy and Schoener 1987; Fisher and Pearcy in press), also appeared to affect the distribution of juvenile coho salmon. During September of 1983 nearly all the seine-captured juvenile coho were taken along our northernmost transect, off Cape Flattery, WA (Fig. 2). In other years juvenile coho salmon during late summer were common and more equally distributed from the Columbia River northward. In the summer of 1983 juvenile coho salmon may have moved farther north, or more likely those to the south may have experienced higher mortality, as a result of northerly currents (Huyer and Smith 1985), warm temperatures and low productivity (Pearcy et al. 1985; Chung 1985) that prevailed off Oregon.

Recoveries of CWT Juvenile Fish in Ocean Fisheries

Data on ocean location of landings of juvenile CWT coho salmon reported in sports and commercial fisheries in the ocean along the west coast of North America, 1977–83, provide valuable information on ocean migrations of marked fish, although these data are biased by differences in legal minimum sizes, time and duration of open season, and effort in the different regions. The summary of all years shows that, except for California, most of the recoveries of juvenile coho salmon during their first summer in the ocean were in the general region of their ocean entry location (Table 6). Both the actual number of fish reported and the estimated total numbers (in parentheses) support our earlier conclusion that many juvenile coho salmon off Oregon and Washington are not highly migratory. All (20) of the actual recoveries of marked juvenile coho salmon that were released in southeastern Alaskan waters were from southeastern Alaska. Ninety-seven percent of the recoveries of marked fish released in British Columbia waters were landed in British Columbia; only two were landed in Alaska. Most (86%) marked juvenile fish from Puget Sound hatcheries were caught in the Sound, and more were recovered in British Columbia fisheries (13%) than in coastal Washington fisheries (<1%), probably due to the smaller size limits for coho in British Columbia as well as migratory patterns. Half of the actual numbers of recoveries of juvenile coho salmon liberated into Washington coastal waters were landed in Washington coastal ports, followed by British Columbia (29%) and the Columbia River region (17%). Only one was landed in Alaska and two in Oregon ports (Garibaldi and south). Juvenile coho salmon originating from Columbia River hatcheries had a broader distribution of recoveries in other regions. Only 40% of Columbia River fish were caught in this region, 41% were taken in northern regions, including two (1%) in Alaska. The remaining 19% were captured off Oregon. The majority (73%) of Oregon coastal fish were recovered off Oregon, followed by the Columbia River region, Washington coast, and British Columbia. None was reported from Alaska, but 10 (2%) were from California ports. All marked California fish were recovered from the Columbia River region and farther south. Most (87%) were landed in Oregon. The few recoveries of California fish off California is undoubtedly influenced by the larger size limits in this than other fisheries.

TABLE 6.—Recoveries of coded wire tagged juvenile coho in the ocean fisheries 1977–83. Estimated total numbers are in parentheses.

	Landing area						
Release area	S.E. Alaska	British Columbia[1]	Puget Sound	Washington Coast (Areas 2–4)	Columbia River (Area 1 + Astoria)	Oregon Coast (Garibaldi and south)	California
S.E. Alaska	20 (39)	0	0	0	0	0	0
British Columbia	2 (2)	1,086 (1,735)	24 (90)	2 (8)	0	0	0
Puget Sound	0	201 (729)	1,352 (5,262)	9 (40)	1 (2)	2 (9)	0
Washington Coast	1 (5)	71 (316)	7 (42)	125 (451)	42 (151)	2 (77)	0
Columbia River	2	24 (133)	4 (14)	39 (162)	67 (310)	31 (164)	0
Oregon Coast	0	18 (107)	3 (13)	21 (83)	62 (213)	308 (1,137)	10 (45)
California	0	0	0	0	1 (4)	138 (552)	19 (200)

[1]Sports catches are not expanded. The estimated total number = expanded commercial catch + actual number CWT's recovered in the sports fisheries. Preliminary data.

In general, the legal size limits increased from north to south, which could result in more recoveries of juvenile coho salmon in northern than southern regions. Thus, these data do not provide evidence that a large proportion of juvenile coho salmon from British Columbia and waters to the south made northward migrations into Alaskan waters before or during the commercial and sports salmon seasons. Movements of Washington, Columbia River, and Oregon fish into British Columbian waters were common however.

Hunter (1985) expanded the catches of CWT juvenile coho salmon caught along the west coast of North America during 1978–80 to the total landed plus estimated "drop-off" mortality (fish that were hooked and died without being landed) of both tagged and untagged hatchery groups. Calculations of the percentage returns from different release and recapture areas are similar to ours (Table 6). The highest percentage of returns were from the areas of release for all areas except for California, and a higher proportion of the catches of Washington coastal, Puget Sound, Columbia River, and Oregon coastal stocks were reported north than south of the area of release.

Are Juvenile Coho Highly Migratory?

Based on our observations on movements of marked fish, north-south and seasonal trends in abundance and size, and directional purse seine sets during the summer, we conclude that many juvenile coho salmon from Oregon and Washington coastal streams and the Columbia River are transported by currents to the south in May and June but then migrate north later in the summer. The mean catches per set of yearling coho salmon in August and September are a large fraction of those in June, indicating that in the years studied many juvenile coho salmon in coastal waters of Oregon and Washington were not highly migratory. Moreover, more marked juvenile hatchery coho salmon were caught in ocean fisheries in the region of release than in distant waters. Recoveries of juvenile coho salmon released from hatcheries south of Cape Flattery were rare in northern waters off Alaska and relatively few were recovered in British Columbia (Table 6). In addition, the positive correlation between upwelling off Oregon and survival of hatchery coho salmon from the Columbia River, Oregon, and California (Nickelson 1986) also argues for a close coupling of OPI coho salmon with a local, not a distant, environmental event during the time that year-class survival is determined. All of these trends suggest that most juvenile coho salmon from this area are not highly migratory and that many usually remain in coastal waters near their sites of ocean entry during their first summer in the ocean, and perhaps during their entire ocean life. In years of unfavorable ocean conditions, however, movements may be more extensive or mortality may be higher, as suggested by the very low catches of juvenile coho salmon in purse seine sets south of Cape Flattery during September 1983, the year of the recent strong El Niño.

Although Pacific salmon are renown for their long foraging migrations in the subarctic Pacific, coho salmon demonstrate both nonmigratory and highly migratory behavior. Milne (1950) found immature coho salmon almost year-round in Georgia Strait and concluded that two types of coho salmon exist in British Columbia waters: "ocean" and "inshore" types, the "ocean" type spending most of its ocean life in coastal and offshore waters and the "inshore" type in inside waters such as Georgia Strait. Healey (1978) caught "inshore" juvenile coho salmon in purse seines in Georgia Strait during summer, fall, and winter months. Similarily, large numbers of coho salmon originating from streams of Puget Sound remain in the Sound throughout their marine life (Haw et al. 1967). Young coho salmon have also been found in the winter and spring, many months after seawater entry in Yaquina Bay (Myers 1980) and other Oregon estuaries (J. Nicholas[4]). Hartt and Dell (1986), in their impressive study of juvenile salmonids of the northeastern Pacific during 1956–70, recognized these two migratory patterns of coho salmon. They found juvenile coho salmon in waters off Vancouver Island and in the Strait of Juan de Fuca throughout the summer and fall, and concluded that some coho salmon spend their entire marine life in "inside" waters and make only limited ocean migrations.

What Proportion of Juvenile Coho from Oregon and Washington Migrate North?

The tagging experiments reported by Hartt and Dell (1986) and Godfrey (1965) provide convincing evidence for long-distance migrations of coho

[4]J. Nicholas, Oregon Department of Fish and Wildlife, Corvallis, OR, 97331, pers. commun. May 1986.

salmon during their first summer in the ocean. Based on recoveries of maturing coho salmon that were tagged a year earlier at sea during April–October 1956–70, Hartt and Dell (1986) concluded that juvenile coho salmon from the Columbia River, Oregon, and California may form a large proportion of the coho stocks that migrate north along the coast each summer. Of the 70 recoveries of tagged fish that were released between Kodiak Island and 56°N, 37% were recovered the following year in the area of the Columbia River and Oregon-California; of the 59 recoveries of fish released between 56°N and Cape Flattery, 47% were recovered in these southern regions. In all, 25% of the recoveries were from Oregon-California, 16% from the Columbia River, 14% from Washington, 33% from British Columbia, and 12% from Alaska.

Loeffel and Forster (1970) concluded that patterns of radioactive ^{65}Zn in juvenile coho salmon collected in the northeastern Pacific supported the concept of a northerly migration from Oregon and Washington into the Gulf of Alaska during the summer. They found that juvenile coho salmon captured off the west coast of Vancouver Island in June and July 1967 contained ^{65}Zn, presumably originating from neutron activation of Columbia River water used to cool the nuclear reactors at Hanford, WA. ^{65}Zn levels decreased in fish caught farther to the north (54°42′N–58°24′N) in July–September of 1967. The authors thought the low concentrations in northern samples represented background levels and that fish with relatively high levels of ^{65}Zn had associated with the Columbia River plume and subsequently migrated north from the Oregon-Washington region. They found low ^{65}Zn levels in 1968, however, and no pronounced latitudinal gradients. Furthermore, they reported none of the many finmarked juvenile coho salmon released from Oregon and Washington hatcheries in 1967 and 1968 north of Juan de Fuca Strait. Hence their evidence for northward movements of Columbia River or Oregon-Washington coho salmon was equivocal.

During June and July 1984, research was conducted with the NMFS Auke Bay Laboratory in waters from northern California to southwest Alaska from the FV *Pacific Warwind* and *Bering Sea*, both making round hauls with the same size of purse seine, to sample juvenile coho in waters north of Oregon and Washington: 37 sets were made in coastal waters of British Columbia, and 39 were made in coastal waters and 29 in inland waters (bays, inlets, and fjords) of southeastern Alaska. Of the 371 juvenile coho salmon captured in these regions, 77% were caught in inland waters of southeastern Alaska. The seven CWT juvenile coho salmon captured were all from Alaska inland waters and all originated from Alaska hatcheries (Auke Bay Laboratory 1984a). A later cruise in southeast Alaska by the Auke Bay Laboratory in August 1984 caught eight CWT coho salmon, also all from inland waters and from Alaskan hatcheries (Auke Bay Laboratory 1984b).

Of the 14 CWT juvenile coho salmon collected in other purse seines, gill nets, and special troll gear in waters of southeastern Alaska during 1982, 1983, and 1985, 12 originated from Alaska hatcheries and 2 originated from Washington hatcheries (Auke Bay Laboratory 1983; Jaenicke et al. 1984; Orsi et al. 1987). Table 6 shows that only 5 of 25 CWT juvenile coho salmon caught in Alaskan waters during 1977–83 were from hatcheries south of Alaska, indicating that most juvenile coho salmon caught in southeastern Alaska during the summer originated from Alaska and not from southern regions.

Hartt (1980) and Hartt and Dell (1986) recognized that their data did not indicate the proportion of southern stocks that made northerly migrations, but they concluded that a large proportion is probable, since juvenile coho salmon were consistently caught in most seine sets throughout the area sampled. They estimated that the average density of juvenile salmonids in coastal waters between 56°N and 60°N off southeastern Alaska during August and September 1964–68 was 1,500 km^{-2}. The average density of juvenile coho salmon in this area during these two months was only 82 km^{-2} (Hartt and Dell 1986, app. A). During August and September 1981–84, the average density of juvenile coho salmon in our round hauls between Cape Flattery, WA and Cape Arago, OR to 37 km offshore was 350 km^{-2}, several times the estimates of Hartt and Dell for the same months of the year. This suggests that juvenile coho salmon may be found in higher densities off Oregon and Washington than southeastern Alaska during late summer, assuming that distributions and abundances in the late 1960s and early 1980s were similar. This trend for higher abundances of juvenile coho salmon off Oregon and Washington than in coastal waters farther north was also found during July 1984 (Table 7), although average catches off Washington and Oregon were not as

TABLE 7.—Average catches of juvenile coho salmon in purse seines sets in coastal waters along the west coast of North America during July 1984[1,2]

Area	No. per set	No. per km^2
Sitka-Juneau	1.29	68
Ketchikan-Sitka	0.58	3
Cape Scott-Dixon Entrance	1.90	100
Vancouver Is.	1.80	95
Washington	3.76	198
Oregon/No. California	2.59	136

[1]Cruise Report, Drum Seiner FV *Bering Sea*, Coastwide NWAFC/OSU Cooperative Study, Ecology of Juvenile Salmon in Coastal and Inside Waters of Southeast Alaska, 28 June–26 July 1984. NWAFC Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 115, Auke Bay, AK 99821.

[2]Fisher and Pearcy (1984).

large as in some earlier years owing to low survival (Fig. 2; Pearcy 1984; Fisher and Pearcy in press).

Comparisons of the estimates of total juvenile yearling coho salmon abundances off Oregon and Washington with the production of coho smolts in the Oregon Production Area (Columbia River to California) also suggests that many juvenile coho resided off Oregon and Washington during the summer. By expanding our catches per m^2 to the region sampled, we estimated that the numbers of juvenile yearling coho salmon in areas surveyed by our purse seine sampling during August or September 1981–84 were 6.3%, 6.5% 5.1%, and 5.2%, respectively, of the numbers of hatchery and wild smolts released in the Columbia River and in Oregon (T. Lichatowich[5]). The areas included in these estimates were roughly 83%, 62%, 51%, and 68% of the total area from Cape Flattery to Cape Arago out to 37 km offshore. Recognizing that the entire area was not sampled, that year-class strength of coho salmon in this region is probably established soon after ocean entrance (Fisher and Pearcy in press), and that early marine mortality may be inversely related to size (Parker 1968; Ricker 1976) so that much of the ocean mortality has occurred by late summer, these percentages probably represent a substantial portion of the surviving OPI coho smolts. In fact, they are several times higher than the smolt-to-adult survival of 1.3–2.8% for OPI public hatchery coho salmon (excluding Rogue River and California hatcheries) during 1981–84 (R. Kaiser[6]).

[5]T. Lichatowich, Oregon Department of Fish and Wildlife, P.O. Box 59, Portland, OR 97207, pers. commun. September 1987.

[6]R. Kaiser, Oregon Department of Fish and Wildlife, Hatfield Marine Science Center, Newport, OR 97265, pers. commun. September 1987.

We conclude, therefore, that a major fraction of the juvenile coho salmon from Oregon and Washington hatcheries did not undertake distant migrations into the Gulf of Alaska in recent years. This is not necessarily in conflict with Hartt and Dell's (1986) data, since they established the presence of Oregon and Washington coho salmon in northern waters but not the proportion of total production that undertakes this migration. On the other hand, neither the stocks of coho nor oceanographic conditions have remained constant over the period from 1956 to 1985 when these two studies were conducted. Wild coho smolts exceeded hatchery smolts in the Oregon Production Area before 1961 (Nickelson 1986) but comprised <12% of the smolts in 1980–85 (R. Kaiser fn. 6). Perhaps wild smolts from the OPI area had different migratory patterns than hatchery smolts do today and migrated rapidly into northern waters soon after ocean entrance. This may explain Nickelson's (1986) finding that survival of hatchery, but not wild coho smolts, was significantly correlated with coastal upwelling off Oregon.

Ocean conditions have also changed over this period. The late 1960's were accompanied by strong upwelling along the coast compared to weak upwelling in the early 1980's (Nickelson 1986; Mason and Bakun 1986). McLain (1984), Norton et al. (1985), and Royer (1985) illustrated that sea surface temperatures and sea levels increased in the northeastern Pacific between 1976 and 1984. These factors and associated changes in ocean circulation could explain differences in migratory behavior of coho salmon between 1960's and 1980's. If currents provide orientational cues to migration, cues facilitating northerly movements may be reduced during years of weak upwelling and weak Ekman transport from the north. Ocean conditions may have modified migratory patterns, as they possibly have for the migration of Fraser River sockeye salmon around Vancouver Island (Groot et al. 1984; Hamilton 1985).

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LITERATURE CITED

AUKE BAY LABORATORY.
1983. Cruise report. NOAA fishery research vessel *John N. Cobb*, JC-83-03. Juvenile salmon purse seining project in coastal and inside waters of southeastern Alaska. NWAFC Auke Bay Lab., Natl. Mar. Fish. Serv., NOAA, 30 p.
1984a. Cruise report drum seines. F/V *Bering Sea*. Coastwide NWAFC/OSU Cooperative study. Ecology of juvenile salmon in coastal and inside waters of southeastern Alaska, 28 June–26 July 1984. NWAFC Auke Bay Lab., Natl. Mar. Fish. Serv., NOAA, 9 p.
1984b. Cruise report, NOAA RV *John N. Cobb* Cruise 84-03. Juvenile salmon purse seining project in coastal and inside waters of southeastern Alaska, July 31–August 31, 1984. NWAFC Auke Bay Lab., Natl. Mar. Fish. Serv., NOAA.

CHUNG, A.
1985. Relationships between oceanographic factors and the distribution of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington, 1982–83. M.S. Thesis, Oregon State Univ., Corvallis, 116 p.

CLUTTER, R. I., AND L. E. WHITESEL.
1956. Collection and interpretation of sockeye salmon scales. Int. Pac. Salmon Comm. Bull. 9:1–159.

DAWLEY, E. M., R. D. LEDGERWOOD, T. H. BLAHM, C. W. SIMS, J. T. DURKIN, R. A. KIRN, A. E. RANKIS, G. E. MONAN, AND F. J. OSSIANDER.
1986. Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966–1983. Final Report, Bonneville Power Administration Project No. 81-102. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, 256 p.

DAWLEY, E. M., R. D. LEDGERWOOD, AND A. JENSEN.
1985. Beach and purse seine sampling of juvenile salmonids in the Columbia River estuary and ocean plume, 1977–1983. Vol. 2: Data on marked fish recoveries. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-75, 397 p.

DAWLEY, E. M., C. W. SIMS, R. D. LEDGERWOOD, D. R. MILLER, AND J. G. WILLIAMS.
1981. A study to define the migrational characteristics of chinook and coho salmon in the Columbia River estuary and associated marine waters. Final Rep. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 68 p.

FISHER, J. P., AND W. G. PEARCY.
1984. Studies of juvenile salmonids off northern California, Oregon, Washington and Vancouver Island. 1984. Oreg. State Univ. Sea Grant Coll. Program (ORESU-T-001), 24 p.
1985. Studies of juvenile salmonids off the Oregon and Washington coast, 1985. Oreg. State Univ. Sea Grant Coll. Program (ORESU-T-004), 31 p.
In press. Growth of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington, USA in years of differing coastal upwelling. Can. J. Fish. Aquat. Sci.

FISHER, J. P., W. G. PEARCY, AND A. W. CHUNG.
1982. Studies of juvenile salmonids off the Oregon and Washington coast, 1982. Oreg. State Univ. Sea Grant Coll. Program (ORESU-T-83-003), 41 p.
1983. Studies of juvenile salmonids off the Oregon and Washington coast, 1983. Oreg. State Univ. Sea Grant Coll. Program (ORESU-T-001), 29 p.

FOESTER, R. E.
1968. The sockeye salmon *Oncorhynchus nerka*. Fish Res. Board Can. Bull. 162, 422 p.

FRENCH, R. R., R. G. BAKKALA, AND D. F. SUTHERLAND.
1975. Ocean distribution of stocks of Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdnerii*, as shown by tagging experiments. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF 689, 89 p.

GODFREY, H.
1965. Salmon of the North Pacific Ocean. Part IX Coho, chinook and masu salmon in offshore waters. 1. Coho salmon in offshore waters. Int. North Pac. Fish. Comm. Bull. No. 16, 39 p.

GODFREY, H., K. A. HENRY, AND S. MACHIDORI.
1975. Distribution and abundance of coho salmon in offshore waters of the North Pacific Ocean. Int. North Pacific Fish. Comm. Bull. No. 31, 80 p.

GROOT, C., L. MARGOLIS, AND R. BAILEY.
1984. Does the seaward migration of Fraser River sockeye salmon (*Oncorhynchus nerka*) smolts determine the route of return of adults? *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill (editors), Mechanisms of migration in fishes, p. 283–292. Plenum Press, N.Y.

GUNSOLUS, R. T.
1978. The status of Oregon coho and recommendations for managing the production, harvest, and escapement of wild and hatchery reared stocks. Oreg. Dep. Fish. Wildl. Fish Div. Proc. Rep., 59 p.

HAMILTON, K.
1985. A study of the variability of the return migration route of Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. J. Zool. 63:1930–1943.

HARTT, A. C.
1975. Problems in sampling Pacific salmon at sea. Int. North Pac. Fish. Comm. Bull. 32:165–231.

1980. Juvenile salmonids in the oceanic ecosystem—the critical first summer. *In* W. J. McNeil and D. C. Himsworth (editors), Salmonid ecosystems of the North Pacific, p. 25–57. Oreg. State Univ. Press.

HARTT, A. C., AND M. B. DELL.
1986. Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. Int. North Pac. Fish. Comm. Bull. 46:1–105.

HAW, F., H. O. WENDLER, AND G. DESCHAMPS.
1967. Development of Washington State salmon sports fishery through 1964. Wash. Dep. Fish. Res. Bull. 7, 191 p.

HEALEY, M. C.
1978. The distribution, abundance, and feeding habits of juvenile Pacific salmon in Georgia Strait, British Columbia. Dep. Fish. Environ. Can., Fish. Mar. Serv. Tech. Rep. No. 788, 49 p.

HICKEY, B. M.
1979. The California Current System - hypotheses and facts. Prog. Oceanogr. 8:191–279.

HUNTER, M. A.
1985. The 1976–1978 brood coho model. Wash. Dep. Fish. Prog. Rep. No. 222, 146 p.

HUYER, A.
1983. Coastal upwelling in the California Current System. Prog. Oceanogr. 12:259–284.

HUYER, A., R. O. PILLSBURY, AND R. L. SMITH.
1975. Seasonal variation of the alongshore velocity field over the continental shelf off Oregon. Limnol. Oceanogr. 20:90–95.

HUYER, A., AND R. L. SMITH.
1985. The signature of El Niño off Oregon, 1982–1983. J. Geophy. Res. 90:7133–7142.

HUYER, A., E. J. C. SOBEY, AND R. L. SMITH.
1979. The spring transition in currents over the Oregon continental shelf. J. Geophy. Res. 84:6995–7011.

JAENICKE, H. W., R. D. BRODEUR, AND T. FUJII.
1984. Exploratory gillnetting from the Oshoro-Maru for juvenile salmonids off southeastern Alaska, 24–25 July 1982. Bull. Fac. Fish. Hokkaido Univ. 35:154–160.

JOHNSON, S. L.
1984. The effects of the 1983 El Niño on Oregon's coho and chinook salmon. Oreg. Dep. Fish Wild. Info. Rep. 84-8, 40 p.

KUNDU, P. K., AND J. S. ALLEN.
1976. Some three-dimensional characteristics of low-frequency fluctuations near the Oregon coast. J. Phys. Oceanogr. 6:181–199.

LOEFFEL, R. E., AND W. O. FORSTER.
1970. Determination of movement and identity of stocks of coho salmon in the ocean using the radionuclide zinc-65. Res. Rep. Fish Comm. Oreg. 2:1–12.

LORD, G., W. C. ACKER, A. C. HARTT, AND B. J. ROTHSCHILD.
1976. An acoustic method for high-seas assessment of migrating salmon. Fish. Bull., U.S. 74:104–111.

MACHIDORI, S.
1966. Vertical distribution of salmon (Genus *Oncorhynchus*) in the North-western Pacific. Hokkaido Reg. Fish. Res. Lab. 31:11–17.

MANZER, J. I.
1964. Preliminary observations on the vertical distribution of Pacific salmon (Genus *Oncorhynchus*) in the Gulf of Alaska. J. Fish. Res. Board Can. 25:1085–1089.

MASON, J. E., AND A. BAKUN.
1986. Upwelling index update, U.S. West Coast, 33N–48N latitude. U.S. Dep. Commer., NOAA Tech. Memo. NMFS No. 67, 81 p.

MCLAIN, D. R.
1984. Coastal ocean warming in the Northeast Pacific, 1976–83. *In* W. G. Pearcy (editor), The influence of ocean conditions on the production of salmonids in the North Pacific, p. 61–86. Oreg. State Univ. Sea Grant Coll. Program (ORESU-W-001).

MCCARL, B. A., AND R. B. RETTIG.
1983. Influence of hatchery smolt releases on adult salmon production and its variability. Can. J. Fish. Aquat. Sci. 40:1880–1886.

MCGIE, A. M.
1984. Evidence for density dependence among coho salmon stocks in the Oregon Production Index area. *In* W. G. Pearcy (editor), The influence of ocean conditions on the production of salmonids in the North Pacific, p. 37–49. Oreg. State Univ. Sea Grant Coll. Program (ORESU-W-83-001).

MILLER, D. R., J. G. WILLIAMS, AND C. W. SIMS.
1983. Distribution, abundance and growth of juvenile salmonids off Oregon and Washington, summer 1980. Fish Res. 2:1–17.

MILNE, D. J.
1950. The difference in the growth of coho salmon on the east and west coasts of Vancouver Island in 1950. Fish. Res. Board Can. Prog. Rep. Pac. Coast Biol. Sta. 85:80–82.

MYERS, K. W. W.
1980. An investigation of the utilization of four study areas in Yaquina Bay, Oregon, by hatchery and wild juvenile salmonids. M.S. Thesis, Oregon State Univ., Corvallis, 234 p.

NICKELSON, T. E.
1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production Area. Can. J. Fish. Aquat. Sci. 43:527–535.

NORTON, J., D. MCLAIN, R. BRAIN, AND D. HUSBY.
1985. The 1982–83 El Niño event off Baja and Alta California and its effect on ocean climate context. *In* W. S. Wooster and D. L. Fluharty (editors), El Niño North, p. 44–72. Univ. Wash. Sea Grant Program.

OREGON DEPARTMENT OF FISH AND WILDLIFE.
1982. Comprehensive plan for production and management of Oregon's anadromous salmon and trout. Part II. Coho salmon plan. Oreg. Dep. Fish Wildl., var. p.

ORSI, J. A., A. G. CELEWYCZ, D. G. MORTENSEN, AND K. A. HERNDON.
1987. Sampling juvenile chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) by small trolling gear in the northern and central regions of southeastern Alaska, 1985. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-115, 47 p.

PACIFIC FISHERIES MANAGEMENT COUNCIL.
1986. Preseason Report 1. Stock abundance analysis for 1986 ocean salmon fisheries. Pac. Fish. Manage. Counc., var. p.

PACIFIC MARINE FISHERIES COMMISSION.
1980. 1977 Pacific salmonid coded wire tag recoveries. Regional Mark Processing Center for Pacific Coast States, Portland, OR.
1981. 1978 Pacific salmonid coded wire tag recoveries. Regional Mark Processing Center for Pacific Coast States, Portland, OR.
1984a. 1979 Pacific salmonid coded wire tag recoveries. Regional Mark Processing Center for Pacific Coast

States, Portland, OR.

1984b. 1980 Pacific salmonid coded wire tag recoveries. Regional Mark Processing Center for Pacific Coast States, Portland, OR.

1984c. 1981 Pacific salmonid coded wire tag recoveries. Regional Mark Processing Center for Pacific Coast States, Portland, OR.

1985a. 1982 Pacific salmonid coded wire tag recoveries. Regional Mark Processing Center for Pacific Coast States, Portland, OR.

1985b. 1983 Pacific salmonid coded wire tag recoveries. Regional Mark Processing Center for Pacific Coast States, Portland, OR.

PARKER, R. R.

1968. Marine mortality schedules of pink salmon of the Bella Coola River, Central British Columbia. J. Fish. Res. Board Can. 25:757–794.

PEARCY, W. G.

1984. Where do all the coho go? The biology of juvenile coho salmon off the coasts of Oregon and Washington. *In* W. G. Pearcy (editor), Influence of ocean conditions on the production of salmonids in the North Pacific, p. 50–60. Oreg. State Univ. Sea Grant Coll. Program (ORESU-W-83-001).

PEARCY, W. G., R. D. BRODEUR, J. M. SHENKER, W. W. SMOKER, AND Y. ENDO.

In press. Food habits of Pacific salmon and steelhead trout, midwater trawl catches, and oceanographic conditions in the Gulf of Alaska, 1980–1985. Bull. Ocean Res. Inst. Univ. Tokyo.

PEARCY, W., J. FISHER, R. BRODEUR, AND S. JOHNSON.

1985. Effects of the 1983 El Niño on coastal nekton off Oregon and Washington. *In* W. S. Wooster and D. L. Fluharty (editors), El Niño North, p. 188–204. Univ. Wash. Sea Grant Program.

PEARCY, W. G., AND A. SCHOENER.

1987. Changes in the marine biota coincident with the 1982–1983 El Niño in the northeastern subarctic Pacific Ocean. J. Geophys. Res. 92, No. C13:14417–14428.

PETERMAN, R. M., AND R. D. ROUTLEDGE.

1981. Experimental management of Oregon coho salmon (*Oncorhynchus kisutch*): Designing for yield of information. Can. J. Aquat. Sci. 40:1212–1223.

PHINNEY, D. E., D. M. MILLER, AND M. L. DAHLBERG.

1967. Mass-marking young salmonids with fluorescent pigment. Trans. Am. Fish. Soc. 96:157–162.

RICKER, W. E.

1976. Review of the growth rate and mortality of Pacific salmon in salt water, and non-catch mortality caused by fishing. J. Fish. Res. Board Can. 33:1483–1524.

ROYER, T. C.

1985. Coastal temperature and salinity anomalies in the northern Gulf of Alaska, 1970–84. *In* W. S. Wooster and D. L. Fluharty (editors), El Niño North, p. 107–115. Univ. Wash. Sea Grant Program.

SCARNECCHIA, D. L.

1981. Effects of streamflow and upwelling on yield of wild coho salmon (*Oncorhynchus kisutch*) in Oregon. Can. J. Fish. Aquat. Sci. 38:471–475.

SUSUKI, T., AND H. SONODA.

1972. On a trial fish finder for salmon and its experimental results. Bull. Jpn. Soc. Sci. Fish. 38:463–469.

WAKEFIELD, W. W., J. P. FISHER, AND W. G. PEARCY.

1981. Studies of juvenile salmonids off the Oregon and Washington coast, 1981. Oreg. State Univ. Sea Grant College Program Ref. 81–13, 51 p.

WARE, D. M.

1978. Bioenergetics of pelagic fish: Theoretical change in swimming speed and ration with size. J. Fish. Res. Board Can. 35:220–228.

WEIHS, D.

1973. Optimal fish cruising speed. Nature 245:48–50.

EARLY MARINE LIFE OF ATLANTIC SALMON, *SALMO SALAR*, POSTSMOLTS IN THE NORTHERN GULF OF ST. LAWRENCE

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ABSTRACT

Postsmolts of Atlantic salmon, *Salmo salar*, having spent some 2–4 months in the marine environment were collected in the nearshore zone of the northern Gulf of St. Lawrence. From a back-calculated smolt length of 135 mm they had increased in length to 265 mm (212 g) on 1 September, and 306 mm (320 g) on 30 September. The rate of increase in length averaged 1.65 mm/day over more than 2 months. Individuals reached 35 cm and 500 g in late autumn. Postsmolts moved in small shoals near the surface and were possibly more active at dawn and dusk. In midsummer, stomach contents changed from insects and gammarids to sand lance, 40–100 mm in length; vertically migrating crustaceans also occurred in the stomachs in autumn. River origin of these postsmolts is not known. The possibility of their belonging to a particular subgroup of some north shore stocks is examined in relation to scale patterns and size of gonads. This occurrence of postsmolts near shore in late summer and presumably their late movement out of the Gulf of St. Lawrence indicate the directional nature of smolt migration to distant feeding areas should be reconsidered. Low sea temperature is hypothesized to trigger the movement out of the Gulf of St. Lawrence. Continual presence of postsmolts in a shallow layer at the surface could prove to be extremely valuable in forcasting movements and production.

Many papers have been published concerning the biology of Atlantic salmon, *Salmo salar*, but very little has been said concerning the postsmolt stage. This stage has been defined as ". . .the juvenile salmon from the time that it leaves the river as a smolt until the onset of wide annulus formation on the scales at the end of the first winter in the sea" (Allan and Ritter 1977). This paper presents new data on the Atlantic salmon postsmolts (hereafter referred as postsmolts) in the northern Gulf of St. Lawrence, reviews our current knowledge on the biology of postsmolts, and points to biological and environmental factors potentially limiting the success of their early life in marine environments.

Published data on postsmolts are mainly limited to stocks in the Baltic Sea. Routes of migration have been described based on the locations and time of early recapture from smolt releases in Sweden and Finland (Carlin 1959; Larsson and Ateshkar 1979; Ikonen and Auvinen 1984, 1985; Jutila and Alapassi 1985). Data on predators are limited (Soikkeli 1973; Valle 1985), and most of the material concerns predation on smolts in streams and estuaries (Larsson 1985). Many analyses of stomach contents have been published, particularly on smaller postsmolts (reviewed by Christensen and Larsson 1979; Jutila and Toivonen 1985). Data on rate of growth (Ikonen and Auvinen 1985) and rate of mortality (Carlin 1959) are lacking. However, Baltic salmon spend their entire sea life in the brackish waters of the Baltic and nearly 80% of smolt production originates from hatcheries (Anonymous 1984). Thus the information derived from salmon in the Baltic should be extended to other stocks only with caution.

Publications on postsmolts in the northern Atlantic and Gulf of St. Lawrence mentioned small salmon as bycatches of commercial fisheries and described the distribution of recaptures from smolt release programs. The earliest report on postsmolts in the Gulf of St. Lawrence claimed that small salmon, referred to as "ouananiche" by local fishermen, were regularly taken near shore in herring nets in autumn (Comeau 1909). Kendall (1935) also reported such incidental catches for the New England coast. Elson (1953) recorded a bycatch of more than 1,000 marked postsmolts from one locality in the Bay of Fundy in the period 1951–53 and reported their mean length. There are also limited records of postsmolts taken off France (Vibert 1953) and in the Gulf of St. Lawrence (Caron 1983) from smolts tagged in streams. Recently, information on movements has been derived from tag returns

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of smolts released in spring in New England and caught in summer in Canada (Meister 1984). Rumors of bycatch in herring nets along the coast of the northern Gulf of St. Lawrence in autumn provided an occasion to acquire some knowledge concerning the elusive postsmolt. Production of salmon in the sea may well be limited by the success of smolts in the marine environment.

Materials and Methods

Postsmolts were collected between Baie Trinité and Rivière-au-Tonnerre in the northern Gulf of St. Lawrence, in 1982, 1983, 1984, and 1985 (Fig. 1). Fishermen contacted in summer 1982 collected postsmolts in late summer and autumn as bycatch in herring gill nets. Four of them were asked in 1983 to monitor the catch of postsmolts in experimental gill nets in late-September in 4 locations (Baie Trinité, Rivière Pentecôte, Port Cartier, and Sept-Iles). We also monitored stations in Baie Trinité in 1983 (23 September–11 October), in Baie Trinité and Port Cartier in 1984 (21 August–20 October), and in Sept-Iles in 1985 (20 August–4 October). Finally, smolts and early postsmolts were collected in seines in June and July, during an eel marking program in the estuary of Grande Trinité River at Baie Trinité (Fig. 1).

Fishermen used standard herring gill nets in 1982, but custom-made gill nets were used in 1983, 1984, and 1985. Custom-made gill nets had 5 sections of increasing mesh sizes (50.8, 57.2, 63.5, 69.9, and 76.2 mm stretched) covering the range in mesh sizes of herring gill nets in the northern Gulf of St. Lawrence. Stretched mesh sizes were determined by measuring 10 meshes per section. Sections were 6 m deep and 10 m long. In 1983, 1984, and 1985, postsmolts were recorded by section individually. In 1984 and 1985, their position in the nets was recorded more precisely: floating lines had numbered buoys and a string divided the nets into 2 halves horizontally. Time of the catch was also recorded. The gill nets were usually visited at 2-h intervals between 0600 and 1800, as sea conditions allowed. They were left fishing overnight. Gill nets were all set at the surface and near shore (<2 km). Mean air temperatures for 1982 to 1985 were drawn from Environment Canada meteorological summaries for Sept-Iles airport. Temperature recorders were also tied to nets in 1983, 1984, and

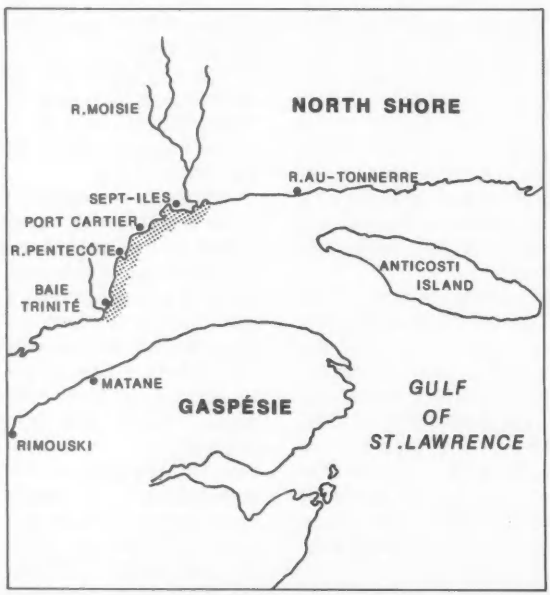

FIGURE 1.—Locations of the areas investigated in the northern Gulf of St. Lawrence (shaded area).

1985 to get hourly records of temperature near the surface, but portions of these records are missing.

Fish were preserved at −15°C for less than 4 months in 1982 and less than 2 months in 1983, 1984, and 1985. Fork length was measured to nearest mm and weight to nearest g. Condition index values were calculated as

$$CI = \sin^{-1}\left[\frac{100 \cdot W}{L^s}\right]^{0.5}$$

CI = condition index; W = weight (g); L = length (mm); s = slope of the length-weight relationship for age groups combined. Scales, usually taken below the dorsal fin close to the lateral line, were cleaned and mounted on glass slides. Stomachs were preserved in formalin (10%) or alcohol (70%) to be analyzed later for their contents. The sex was determined visually and checked histologically on a subsample of postsmolts collected in 1982. Gonads were weighed to nearest mg and only in 1982. Gonadosomatic index (GSI) was calculated as

$$GSI = \frac{GW}{TW - GW} \cdot 100$$

where GW = gonad weight; TW = total weight.

Scales showing no focal regeneration were examined for age determination by 2–4 readers. Readings were discussed and a consensus was reached in most cases. Reported ages are smolt ages plus 2–4 months. Fork length at smoltification (mm) was back-calculated as

$$LS = \left[\frac{(LC - 34) \cdot RS}{RC}\right] + 34$$

where LS = back-calculated smolt length; LC = body length of post smolt; RS = scale radius at smolt check; RC = scale radius of postsmolt. Length at scale formation is assumed to be 34 mm. Scales were also examined for any mark in the postsmolt zone that could be of potential interest. Hence the number of individuals showing a transition zone between the riverine and marine increments was determined in 1982, and the number of individuals showing a summer check was determined in 1982, 1983, 1984, and 1985. Scale radii were measured along the postero-anterior axis on 4 scales per individual in 1982, and on 1 scale per individual in 1983, 1984, and 1985. Projected scales were measured at constant magnification on a digitizing pad connected to a personal computer. Fork length at formation of a summer check (mm) was back-calculated for 1982 and 1983 as

$$LF = \left[\frac{(LC - 34) \cdot RM}{RC}\right] + 34$$

where LF = back-calculated length; LC = body length of postsmolt; RM = scale radius at summer check; RC = scale radius of postsmolt.

Stomach contents were examined in detail in 1982. Results are expressed as percentage of occurrence (number of stomachs containing an item divided by the number of stomachs examined) and percentage by number (the count number of an item divided by the count number of all items). Food items that could not be identified are referred to as remains. In as far as their condition allowed, prey fish were usually measured to the nearest cm. Stomach contents examined in 1983, 1984, and 1985 were consistent with the 1982 conclusions, so the results are not presented.

Results

The Age and Sex Composition

Three-year-old female salmon dominated the catch both in 1982 and 1983 (Table 1). Postsmolts ranged from 2 to 5 years in 1982 and from 2 to 4 years in 1983. Five-year-old salmon made up less than 4% of the catch in 1982. Three-year-old and, to a lesser extent, 4-yr-old salmon dominated the catch both in 1982 and 1983 (82% of the catch); mean smolt age was 3.2 ± 0.7 years. Age composition in 1983 differed from 1982 because of an increase in the percentage of 2-yr-old salmon (12% to 21%) and a decrease in the percentage of 5-yr-old salmon ($\chi^2 = 15.96$, $P < 0.01$). The sex ratio (male:female) for 1982 and 1983 combined was

TABLE 1.—The age and sex composition of the catch of postsmolt Atlantic salmon along the north shore of the Gulf of St. Lawrence, 1982 and 1983.

		Smolt age				
Year	Sex	2	3	4	5	Total
1982	Female	26	114	79	7	226
	Male	19	67	49	7	142
1983	Female	25	58	15	0	98
	Male	8	26	23	0	57
Total	Female	51	172	94	7	324
	Male	27	93	72	7	199

0.62. This ratio did not change between years ($\chi^2 = 7.92$, $P < 0.01$) and was significantly less than 1.0 (binomial test: $z = -5.37$, $P < 0.001$). There was no trend between sex ratio and smolt age in 1982 ($\chi^2 = 1.21$, $P = 0.75$), but the percentage of males tended to increase with smolt age in 1983 ($\chi^2 = 12.67$, $P = 0.002$).

Length at Smoltification

The mean length at smoltification was estimated by back-calculation at 135 ± 15 mm for postsmolts collected in 1982 and 1983. Scale radius was linearly related to body length both in 1982 (4 scales measured per fish, $P < 0.0001$) and in 1983 (1 scale measured per fish, $P < 0.0001$); probability values are those of F-tests from analysis of variance. Back-calculated smolt lengths were normally distributed ($P = 0.80$): 75% of the postsmolts ranged between 120 and 150 mm at smoltification. There were also 7% individuals in the 160–200 mm range. Differences in mean smolt length were not significant between the ages and the sexes both in 1982 ($F = 1.84$, $P = 0.08$) and in 1983 ($F = 1.05$, $P = 0.39$), and, pooling the ages and the sexes, between 1982 and 1983 ($t = 1.32$, $P > 0.15$).

Rate of Increase in Size

The rate of increase in size of postsmolts was very rapid in summer both in 1982 and 1983. Postsmolts collected in 1982 between mid-August and mid-October ($n = 383$; mean date is 1 September) averaged 265 ± 25 mm (range 195–328) and 212 ± 58 g (range 92–389). In 1983, postsmolts collected between mid-September and mid-October ($n = 155$, mean date is 30 September) averaged 306 ± 17 mm (range 258–362) and 320 ± 57 g (range 192–565). There was no difference in mean size between males and females and between age-classes in 1982 ($P > 0.40$) and 1983 ($P > 0.20$); probability values are those of F-tests from 2-way analysis of variance. From a mean smolt length of 135 mm and assuming smolts migrated to estuaries 15 June, postsmolts grew at a rate of 1.65 mm/day during a 2.5-mo (15 June—1 September) and a 3.5-mo (15 June–30 September) period in 1982 and 1983, respectively.

This estimate is conservative because the rate of increase in length tended to decrease late in the sampling period. Postsmolts steadily increased in length and weight in the period mid-August to mid-September 1982 (Figs. 2, 3). From mid-September, the rate tended to slow down. The inclusion of data for 1983, collected later in the autumn, corroborates this observation indicating that conditions changed in late-September in 1982 and 1983.

Length-weight relationships were examined for 1982 and 1983 separately. The analysis of covariance showed that males and females exhibited the same length-weight relationship, both in 1982 ($P = 0.53$) and 1983 ($P = 0.42$). Similarly, length-weight relationship did not change between age groups in 1982 ($P = 0.06$) and 1983 ($P = 0.49$). The covariance for 1982 was nearly significant because the slope for 5-yr-old postsmolts, based on 15 individuals, was larger than for other age groups. However, mean condition index values by age revealed no significant difference between age groups in 1982 ($P = 0.11$) or 1983 ($P = 0.28$).

Since there was also no significant difference in the length-weight relationship between 1982 and 1983 ($P = 0.14$), the data were pooled. Thus the length-weight relationship for postsmolts collected in this study can be described as a single regression:

$$\log W = (2.8280 \cdot \log L) - 4.5336$$

$$P < 0.001,\ n = 539$$

where W = weight (g); L = length (mm).

Maturation of Gonads

Postsmolts were all immature both in 1982 and 1983, but differences were observed between males and females in 1982. Testes averaged 48 ± 6 mg (95% C.L., $n = 124$) for a mean male gonadosomatic index value of 0.025% ± 0.003% (95% C.L., $n = 124$). There was no significant difference in the mean value of either parameter between age groups ($P > 0.52$). Testis weight increased in time and as body length and body weight increased, but again there was no difference between age groups (Table 2). However, the gonadosomatic index did not change in time ($P = 0.10$) or as postsmolts' size increased ($P = 0.16$ for body length and $P = 0.10$ for body weight), suggesting that changes in size of the testes were not allometric in male postsmolts in the autumn period. Regressions were tested and compared following Snedecor and Cochran (1967) and Sokal and Rohlf (1969).

There was more variability in the data for fe-

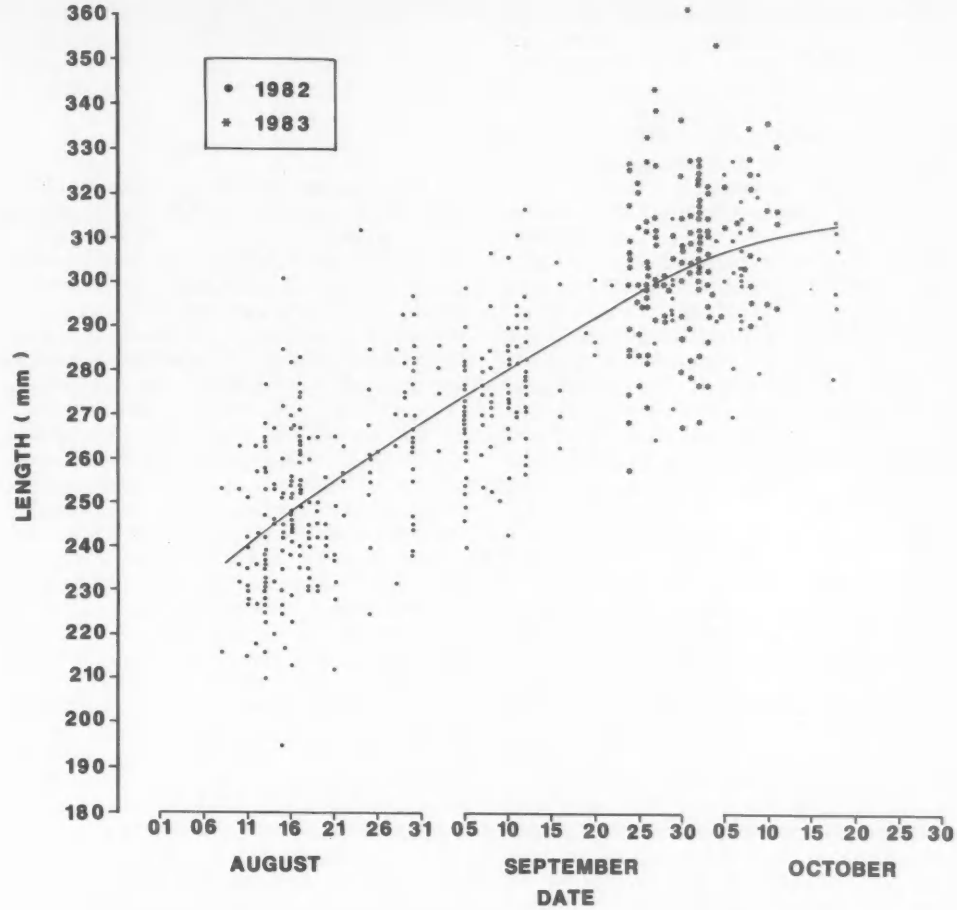

FIGURE 2.—Seasonal changes in length of Atlantic salmon postsmolts collected in 1982 and 1983.

TABLE 2.—Functional regressions of gonad weight on date, body length, and body weight of Atlantic salmon male postsmolts ($n = 124$). Lengths and weights are log-transformed.

	Date	Length (mm)	Weight (g)
Regression	$P < 0.0001$[1]	$P < 0.0001$[2]	$P < 0.0001$[3]
Covariance (age groups)	$P = 0.31$ n.s.	$P = 0.56$ n.s.	$P = 0.47$ n.s.

[1] $Y = 0.0168\ X - 5.4166$.
[2] $Y = 7.8496\ X - 20.3350$.
[3] $Y = 2.6798\ X - 7.5298$.

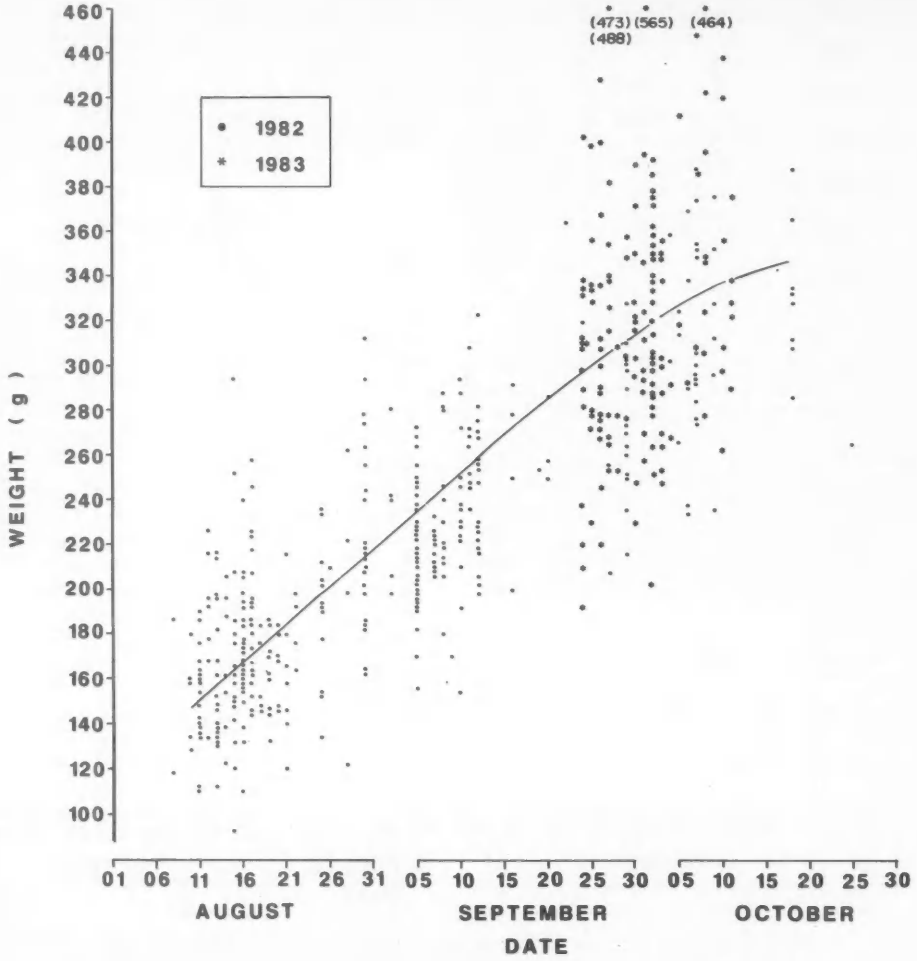

FIGURE 3.—Seasonal changes in weight of Atlantic salmon postsmolts collected in 1982 and 1983.

males. Though the size of ovaries did not differ significantly between age groups ($P = 0.07$), gonadosomatic index values increased in older female postsmolts ($P = 0.0006$). Mean values ranged from 133 mg (0.06%) for 2-yr-old postsmolts to 205 mg (0.10%) for 5-yr-old postsmolts (Table 3). The regressions of ovary weight on body length, body weight, and time were all significant except for 5-yr-old females (Table 4), and differed between age groups particularly in elevation ($P < 0.05$, $n = 213$). The regressions of gonadosomatic index values on the same variables were

TABLE 3.—Gonad weight (mg) and gonadosomatic index (GSI) (%) of Atlantic salmon female postsmolts: mean values and confidence limits ($n = 213$).

Age group	Gonad weight		GSI	
	Mean	95% C.L. interval	Mean	95% C.L. interval
2	133	124–144	0.064	0.060–0.067
3	152	142–163	0.077	0.073–0.082
4	175	161–189	0.092	0.087–0.098
5	205	194–217	0.095	0.091–0.099

not significant indicating that, in females as in males, changes in size of the gonads were not allometric (body length: $P = 0.06$; body weight: $P = 0.73$; time: $P = 0.68$).

Scale Marks

Scales used for age determination were also examined for any mark that could be of use in stock identification. Many individuals exhibited a transition zone on their scales. Circuli in this zone were more wide-spaced than circuli laid down in earlier summers, but they were more narrow-spaced than circuli formed in summer in a marine environment. This mark was present on 73% of the scales in both males and females (72.6 and 73.8%) but tended to decrease as smolt age increased: 84% (age 2 years), 75% (3 years), 68% (4 years), and 62% (5 years). However, the trend was not significant ($\chi^2 = 5.74$, $P > 0.10$).

Scales also exhibited summer checks in 1982, 1983, and 1984. The number of circuli between the smolt mark and the summer check was 10.9 ± 2.6 (mean $\pm$ SD) (range 7–15) in 1982 and 9.7 ± 2.2 (range 5–15) in 1983. The ratio between the radius to summer check and the radius to smolt mark averaged 2.00 ± 0.30 (range 1.49–2.45) in 1982, and 1.67 ± 0.19 (range 1.26–2.32) in 1983. The overall percentage of occurrence was low in 1982 (3.6%) and involved only specimens collected in the area Baie Trinité-Pointe aux Anglais where 11 out of 13 postsmolts examined showed a summer check. The incidence of summer checks on scales increased markedly in 1983 (55%) and 1984 (75%), and summer checks were no longer restricted in distribution. Examination of data concerning postsmolts possessing a summer check showed no relationship between the check and measured biological variables except perhaps in 1982. The gonads of males having a summer check on their scales ($n = 5$) were heavier than in males having no summer check (120 mg and 48 mg respectively). Their gonadosomatic index was also higher (GSI = 0.042% and 0.025% respectively). This was not so in females. Information on gonads is not available for 1983, 1984, and 1985.

Back-calculated lengths at summer check formation were larger in 1982: 22 ± 2.5 cm in 1982 and 20 ± 2 cm in 1983. Postsmolts measured 265 mm on 1 September. With a mean rate of increase in length of 1.65 mm/day, the check must have been formed some 26 (1982) to 40 (1983) days earlier, i.e., in late-July. This is confirmed by extrapolation of the length-date plot (Fig. 2). No salmon were noted possessing 2 summer checks on their scales.

Food Items

Drastic changes took place in prey selection between postsmolts collected in summer and in autumn. The stomach contents of 40 salmon ranging up to 188 mm in length (70 g) collected in the second half of July 1984 in the estuary of the Grande Trinité River, near Baie Trinité, revealed a low diversity in prey items, indicative of a transition period between the riverine and marine environment. Small fish remains were observed in only 5 out of 39 stomachs containing food remains. Invertebrates were observed in 38 stomachs, classes Insecta and Crustacea occurring in 87 and 92% of the stomachs respectively. Food items consisted mainly of 2 families: Chironomi-

TABLE 4. – Functional regressions of gonad weight on date, body length, and body weight of Atlantic salmon female postsmolts ($n = 213$). Lengths and weights are log-transformed.

	Significance	Functional regression
Date	2 : $P = 0.0001$	$Y = 0.0075\ X - 2.7127$
	3 : $P = 0.0001$	$Y = 0.0044\ X - 1.9052$
	4 : $P = 0.0058$	$Y = 0.0052\ X - 2.0229$
	5 : $P = 0.26$ n.s.	
	covariance : $P = 0.04$	
Length (mm)	2 : $P < 0.0001$	$Y = 3.8015\ X - 10.1089$
	3 : $P < 0.0001$	$Y = 2.9105\ X - 7.8659$
	4 : $P < 0.0001$	$Y = 3.1893\ X - 8.4701$
	5 : $P = 0.34$ n.s.	
	covariance : $P = 0.02$	
Weight (g)	2 : $P < 0.0001$	$Y = 1.3110\ X - 3.9428$
	3 : $P < 0.0001$	$Y = 1.0385\ X - 3.2227$
	4 : $P < 0.0001$	$Y = 1.1763\ X - 3.4659$
	5 : $P = 0.28$ n.s.	
	covariance : $P = 0.04$	

dae (95% of insects by number) and Gammaridae (92% of crustaceans by number).

Later in summer and autumn, postsmolts consumed mainly small fish. Stomach contents were analyzed for 373 out of 385 postsmolts collected in 1982. There were 109 stomachs with no food remains (29%). They were most prevalent in the first half of August: 46%, 1–15 August; 25%, 16–31 August; 26%, 1–15 September; 25%, 16 September–31 October. Fishes dominated the list of prey items as they occurred in 238 out of 264 (90%) stomachs containing food remains, including 200 postsmolts (84%) that fed exclusively on small fish. Fishes could be identified in 157 stomachs. Diversity was low, capelin, *Mallotus villosus*, occurring in 16 stomachs (10%) and sand lance, *Ammodytes americanus*, in 145 stomachs (92%). *Ammodytes americanus* dominated in terms of percentage by number (94%). Postsmolts consumed smaller *A. americanus*, in the 40–100 mm range (Fig. 4). Stomachs examined in 1983, 1984, and 1985 confirmed these observations.

Invertebrates were found in 69 out of 264 stomachs (26%) containing food remains. Eighteen postsmolts had only invertebrates in their stomachs (26%). In contrast with smolts in the estuarine environment, postsmolts did not rely on insects; insects occurred in only 8 stomachs (3%), whereas crustaceans occurred in 61 stomachs (23%) (respectively, 12 and 88% by number). Furthermore, the class Amphipoda no longer dominated the crustaceans (Table 5).

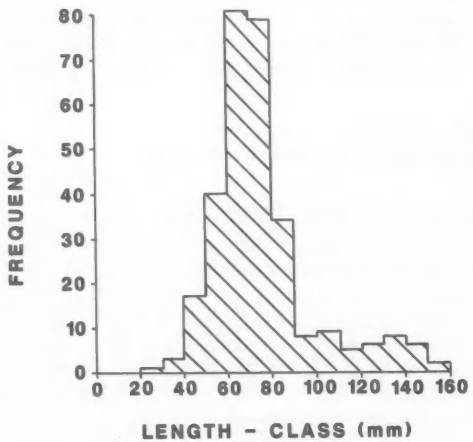

FIGURE 4.—Length distribution of sand lance in the stomachs of Atlantic salmon postsmolts collected in 1982.

Horizontal and Vertical Position in the Nets

Postsmolts were not randomly distributed in the nets in 1984. They occurred most frequently (78% of the individuals) in the top half of the nets (binomial test; $z = 4.62$, $P < 0.001$; Siegel 1956). Furthermore, 25 out of 74 salmon occurred alone in the nets, but many also occurred in clusters. Positions of postsmolts are indicated by number of nearest buoy on the head-line for those sets having taken 2 salmon and more (stations visited at 2-h intervals usually but also nets set overnight) (Table 6). Distributions are likely not random in sets 3, 6, 7, 9, 10, and 11 and most particularly in sets 13 and 15. The catch was low in midday: 3 salmon between 0900 and 1200 and 5 between 1200 and 1500. This increased to 12 between 1500 and 1800. The majority were caught later than 1800 (36) and in the morning between 0600 and 0900 (20).

Finally, positions in the nets were analyzed in terms of selectivity. The gear used in 1982 could not be controlled. Fishermen reported using

TABLE 5.—Crustacean organisms in the stomachs of Atlantic salmon postsmolts collected in the period August–October 1982, based on 39 stomachs containing identifiable crustaceans.

Crustacean order	Percentage of occurrence	Percentage by number	Main organisms
Euphausiacea	87	68	*Meganyctiphanes norvegica* *Thysanoessa inermis* *Thysanoessa raschi*
Decapoda	28	24	*Chionoecetes opilio* (larvae)
Amphipoda	15	8	

TABLE 6.—Positions of Atlantic salmon postsmolts in nets by number of nearest buoy on head-line for catches of 2 salmon and more.

Set no.	No. of smolts	Number of nearest buoy to each smolt
1	2	11 32
2	2	12 23
3	2	14 15
4	2	15 23
5	2	19 27
6	2	22 24
7	2	23 23
8	2	23 39
9	2	25 27
10	2	23 27 27
11	4	16 21 21 43
12	5	16 24 33 42 44
13	5	23 23 23 23 23
14	6	12 17 18 18 22 42
15	9	11 12 12 12 13 13 13 14 14

62 mm stretched mesh nets (range 57–70 mm); mesh size is regulated. The nets used in 1983, 1984, and 1985, had 5 sections of increasing stretched mesh sizes: 50.8, 57.2, 63.5, 69.9, and 76.2 mm. Catches were recorded for individual mesh sizes in 1983 combining the 4 stations. Modal length increased only slightly as mesh size increased. Furthermore, the distribution for the 69.9 mm mesh was skewed to the right, indicating no larger sized postsmolts were present. There was also no catch in the 50.8 mm mesh, but this may have been because of the small mesh section being made of a coarser material in 1983. Postsmolts were frequent (n = 49) in the 57.2 mm mesh, but the distribution for this mesh does not suggest the existence of smaller postsmolts as the size range is similar to that of the 63.5 mm mesh and covers the size range for the 5 meshes combined. Catches declined from a maximum in the 63.5 mm mesh (56) to 40 and 9 in the 69.9 and 76.2 mm mesh, respectively. Therefore it is unlikely that there was any bias except perhaps against smaller postsmolts.

Fall Movement out of Coastal Reaches

Postsmolts gradually left the nearshore area in late-September. Fishermen in 1982 started collecting postsmolts in mid-August. Their bycatch declined from mid-September and was low in October. The catch declined partly because most commercial fishermen were asked to return no more than 20 salmon each, and they reached this limit early (Table 7). Fishing was initiated later in 1983 and took place over a shorter period (23 September–11 October), but a 68% decline in the catch was observed between the period 29 September–5 October and the period 5–11 October. Finally in 1984, postsmolts came near the coast near the end of August and moved out in mid-September (Table 8) so that no salmon were caught in the period 20 September–20 October.

This movement out of the nearshore zone was associated with decreasing near-surface temperatures in autumn. Temperatures measured near the surface closely followed the mean air temperatures recorded in Sept-Iles (Fig. 5). Since most postsmolts travelled near the surface, mean air temperatures were assumed to reflect prevailing conditions for postsmolts. In 1982, postsmolts were abundant until mean air temperatures declined below 5°C, i.e., in early October. The situation was similar in 3 stations out of 4 in 1983, particularly in the Bay of Matamek River near Sept-Iles and in Rivière Pentecôte, 2 stations closer to our monitoring station. In 1984, this decline in mean air temperature occurred earlier (26 September), but surface temperatures were also lower than air temperatures, and the catch declined (Table 8) as soon as surface temperatures fell below 5°C (mid-September.) Hence, low temperatures were associated with a movement of postsmolts out of the nearshore zone. However, the reverse is not true: results for 1983 and 1984 suggest that postsmolts do not necessarily move towards nearshore zones when prevailing temperature conditions are favorable.

Variations in seasonal abundance are masked by a general decline in salmon abundance near shore from 1982 to 1985. Fishing effort could not be assessed in 1982, but the incidence of postsmolts in coastal herring nets in 1982 was such that it can reasonably be concluded they were more abundant than in 1983, 1984, or 1985. Relative abundance can be assessed for 1983, 1984, and 1985. Baie Trinité and Port Cartier stations were operated in 1983 and 1984 using similar nets at the same locations each year and showed that postsmolts were more abundant in 1983 than in 1984 (Table 9). Finally, a station was monitored near Sept-Iles in 1985 in an area where the best catches were made in 1982, using

TABLE 7.—Time distribution of the commercial bycatch of Atlantic salmon postsmolts in 1982.

Period	Number
10–31 August	210
01–15 September	118
16–30 September	21
01–15 October	24
16–31 October	8

TABLE 8.—Catch of Atlantic salmon postsmolts by period and locality in 1984.

	Locality	
Period	Baie Trinité	Port Cartier
21–24 August	1	4
24–27 August	0	0
27–30 August	0	1
30 August–02 September	0	14
02–05 September	4	8
05–08 September	6	9
08–11 September	0	2
11–14 September	3	16
14–17 September	0	8
17–20 September	0	0
20 September–20 October	0	0

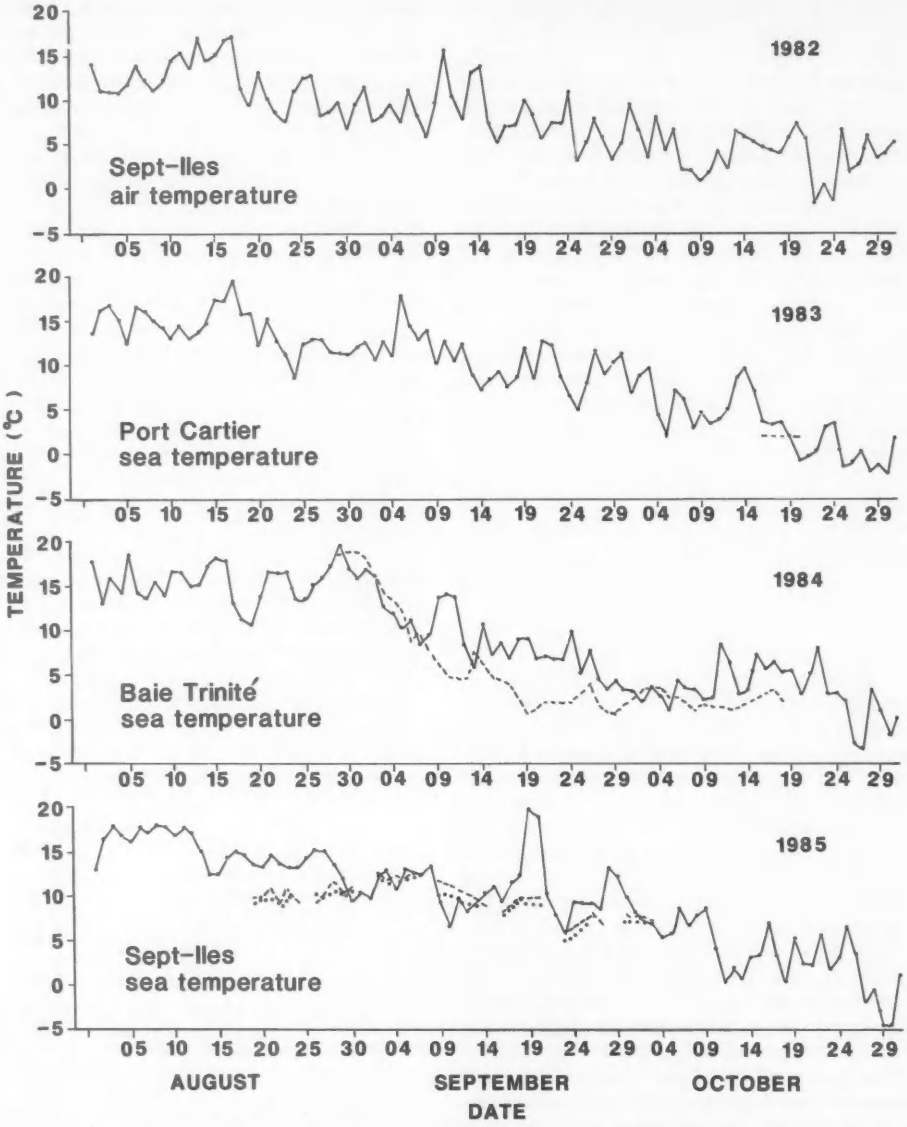

FIGURE 5.—Mean daily air temperature in Sept-Iles (-•-), and mean daily sea temperature at 0.5 m (- - -) in Port Cartier (1983), at 6 m (- - -) in Baie Trinité (1984), and at 0.5 m (- - -) and 6 m (•••••) in Sept-Iles (1985).

TABLE 9.—Relative abundance in terms of catch per unit of effort (CPUE) at 2 stations run in 1983 and 1984 using similar nets at the same sites.

Period	Baie Trinité			Port Cartier		
	Catch	E	CPUE	Catch	E	CPUE
1983						
23 Sept.–11 Oct.	54	38.5	1.4	40	20.0	2.0
1984						
21 Aug.–31 Aug.	1	20.5	0.1	5	32.5	0.2
30 Aug.–17 Sept.	15	54.5	0.3	57	73.0	0.8
17 Sept.–23 Sept.	0	22.0	—	0	17.0	—
23 Sept.–11 Oct.	0	55.5	—	0	45.5	—
11 Oct.–18 Oct.	0	9.5	—	0	21.0	—

[1]CPUE: catch of 1 net in 24 hours.

similar nets to 1983 and 1984. The catch was nearly nonexistent: 5 salmon for 120 unit effort (1 unit effort, is 1 net × 24 hours). Thus, based on limited observations, numbers of salmon near shore in summer and autumn seem to be highly variable from year to year.

DISCUSSION

Postsmolts of Atlantic salmon stay much longer near our coasts than is usually believed. Though early months in the marine environment have been shown to have a marked influence on salmon runs 1 and 2 years later (e.g., Christensen and Larsson 1979; Scarnecchia 1983, 1984), postsmolt biology has been a neglected area of investigation. North American smolts are assumed to migrate rapidly out of the estuaries of their home rivers, to feeding areas located far out in the North Atlantic east of the Grand Bank (Templeman 1968; Reddin 1985) and north to Labrador and Greenland (Saunders 1966; Templeman 1967). They return 1 or 2 years later to spawn in home rivers. This study, and early records, indicate that some postsmolts remain in coastal areas as late as autumn before moving offshore. This was clearly suggested by Comeau (1909) who stated that 0.5–1.5 lb postsmolts were regularly taken in autumn along the north shore of the Gulf of St. Lawrence. Fishermen interviewed in 1982 on the north shore of the Gulf of St. Lawrence, from Pointe-des-Monts to Blanc Sablon, declared incidental catches of postsmolts, mainly in the months of August and September. The majority declared taking postsmolts each year. Smolts were also shown to linger in estuaries of the north shore of the Gulf of St. Lawrence (this study; Power and Shooner 1966; Randall and Power 1979). Huntsman (1939) mentioned their occurrence in autumn in herring nets near the mouth of Gaspé Bay. Fall catches also occurred in New England (Kendall 1935). Recently, smolts released in New England were caught as postsmolts in coastal areas of Canada (Meister 1984). There are stocks in the Bay of Fundy (as the stocks in the Baltic) that do not go on extensive migrations in the North Atlantic (Huntsman 1939; Jessop 1976): postsmolts of these stocks are regularly taken in herring nets in Passamaquoddy Bay and off Grand Manan Island (Elson 1953, 1964; Allen et al. 1972). Hence the presence of postsmolts near shore in autumn (or in summer and autumn) is a characteristic of the marine life of Atlantic salmon in North America. Timing of migration has been described for hatchery-reared smolts released in Sweden (Larsson 1974) and Finland (Jutila and Alapassi 1985). Tags were returned mostly from a distance of less than 10 km between days 0 and 10, 20–50 km between days 10 and 20, and 50–100 km 2 months past their release, in the brackish waters of the Gulf of Bothnia (Jutila and Alapassi 1985).

Behavior of postsmolts is similar to that of 1- and 2-sea-year salmon. Postsmolts in this study occurred mainly near the surface as indicated by their distribution in the nets. LaBar et al. (1978) concluded that smolts migrated near the surface in the Penobscot estuary. Templeman (1967, 1968) also found salmon to occur near the surface in the Northwest Atlantic: 62% occurred in the top 0.6 m and 90% in the top 1.5 m in July and August 1965. Similarly in 1966, most salmon were taken in the top 1.5 m, the number caught decreasing sharply below 0.6 m. Similar observations were made on Baltic salmon (Carlin and Lundin 1967; Christensen 1968). There is less information available on schooling. Postsmolts did not regularly have a clustered distribution in nets, but considering that a net does not retain all the salmon striking it, there were still many instances of salmon moving in schools. Thurow (1968) came to the same conclusion for older salmon in the Baltic. Templeman (1967) presented limited evidence for salmon in the Northwest Atlantic, but reached negative conclusions later (Templeman 1968). Finally there are limited data in the literature concerning the rhythm of activity of salmon in the marine environment. Christensen and Lear (1980) showed that in West Greenland best catches occurred early in the morning (0600–0800), decreased sharply between 0800 and 1000, and were low between 1000 and 1400. The nets were not set between 1400 and

0600. Catches in this study were also low in midday. Either this is a reflection of 2 peaks of activity, dawn and dusk, as is common in salmonids in freshwater, or this is possibly due to salmon avoiding the nets in high light levels. Thus postsmolts and 1- and 2-sea-year salmon appear to have a similar behavior at sea. They move in small schools close to the surface and are possibly more active at dusk and dawn.

Food items in the stomachs of postsmolts changed markedly in summer and indicated a low diversity of prey. This is in contrast to findings reported for salmon in the Northwest Atlantic. Grande Trinité River postsmolts had fed mostly on chironomids and gammarids in late-July. Baltic salmon postsmolts fed mainly on aerial insects though small fish and crustaceans also occurred in the stomachs of postsmolts in the southern Baltic (reviewed by Christensen and Larsson 1979). Jutila and Toivonen (1985) also found aerial insects to be the dominant food items in the stomachs of small postsmolts (<20 cm) in the Gulf of Bothnia (Baltic). They observed that postsmolts were not selective and must have fed near the surface (20 cm surface layer). Postsmolts collected later in the present study relied mainly on small sand lance. Insects and gammarids had been replaced by vertically migrating crustaceans such as *Meganyctiphanes norvegica* (Kulka et al. 1982). Thurow (1968) estimated 25 cm to be the length threshold for piscivorous feeding by Baltic salmon. In the present study, this size was likely reached in the first half of August 1982. This coincides with a major change in stomach contents and a high percentage of stomachs containing no food. The data on postsmolts in July are too limited to suggest that sand lance abundance could limit the early success of postsmolts at sea, but potential relationships in late summer should be tested as was done for capelin by Reddin and Carscadden (1981). Data on 1- and 2-sea-year salmon indicate they will readily feed on a diversity of prey items, main items including Arctic squid, *Gonatus fabricii*; paralepids, *Paralepis coregonoides*; and lantern fishes (*Lampenyctus* sp., *Notoscopelus* sp.) (Templeman 1967, 1968; Lear 1980). Sand lance and capelin are dominant items in West Greenland and on the coast of Newfoundland (Lear 1972, 1980), and on the Grand Bank (Reddin 1985). Reddin (1985) observed major changes in stomach contents between salmon on the Grand Bank (sand lance and capelin) and east of the Grand Bank (Bathylagidae, *Paralepis* sp., and crustaceans), emphasizing that salmon are not selective predators.

The rate of increase in mean length averaged 1.65 mm/day in the Gulf of St. Lawrence over the summer period in 1982 and 1983. This value is based on the hypothesis that smolts migrated to estuaries in mid-June. Smolt migration took place in the first half of June in Restigouche River in the southern Gulf of St. Lawrence (Peppar 1982) and in the second half of June in Grande Trinité River in the northern Gulf of St. Lawrence (Caron 1984). Downstream migration of smolts peaked at various dates in June in Western Arm Brook in western Newfoundland (Chadwick 1981). The calculated rate of increase is also based on a mean back-calculated smolt length of 135 mm. Length at smoltification averaged 125–130 mm in Grande Trinité River (mean and SD: 127.5 ± 12.3, $n = 88$, in 1981; 125.8 ± 10.9, $n = 92$, in 1982; see also Caron 1984). Matamek River and Moisie River smolts measured 125–150 mm (Schiefer 1972). They measured 150 mm in Little Codroy River (Murray 1968) and 174 mm in Western Arm Brook (Chadwick 1981). There are no data in the literature concerning the rate of increase in size of smolts and postsmolts in the marine environment. Postsmolts in the Bay of Fundy reached a mean length of 296 mm in mid-August 1952 (Allen et al. 1972), some 3 cm more than postsmolts in this study: 265 mm and 306 mm on 1 September and 30 September. However the high value of the power exponent of the length-weight relationship as compared with salmon in Newfoundland and Labrador (Lear 1973) indicates postsmolts were not in poor condition. There was possibly a decline in the rate of increase in length in mid-summer as suggested by the large proportion of scales showing a summer check (false-annulus) in 1983. This occurred 10 circuli from the smolt check in mid-summer in postsmolts 20–22 cm in length, i.e., prior to this study period, and may have been produced as a response to a shortage of prey or to deteriorating environmental conditions. Elson (1953) also noticed the frequent occurrence of a slowing of growth 6–10 circuli out from the last parr annulus. The percentage of occurrence of the check varied between locations (1982) and between years (1982 < 1983 < 1984). Therefore it is not likely to be a response to a change in postsmolt biology such as a scheduled shift in prey selection. However, the summer check can be thought of as a potential tool for stock discrimination. Some 26–32 circuli are formed before the first sea an-

nulus is formed (Lear and Misra 1978) at a length of 46–50 cm in the first half of April (Munro 1970).

Presence of postsmolts near shore in late summer in the northern Gulf of St. Lawrence, as reported in this study, and presumably their late movement out of the Gulf of St. Lawrence indicate that the directional nature of the migration should be reconsidered. There are some smolts that do not head towards the high seas as soon as they reach the estuaries. They seem to roam nearby unless prevailing conditions are not favorable. Temperature can be hypothesized as triggering the late movement of postsmolts out of the northern Gulf of St. Lawrence. Saunders (1986) reviewed the thermal biology of Atlantic salmon and suggested the thermal range for salmon in the sea is lower than for juvenile salmon in freshwater. Salmon occur mainly at temperatures ranging from 4° to 8°C in the Northwest Atlantic (Templeman 1968; May 1973; Reddin 1985). Postsmolt movements out of the nearshore area took place in a short period as temperature was decreasing, between mid-September and mid-October. Postsmolts were more abundant in 1982 and 1983 as mean air temperature ranged between 4° and 10°C in early autumn. In 1984, sea temperature decreased rapidly from more than 15°C in late-August down to 2°C in mid-September; postsmolts vanished from the nearshore area as temperature declined below 4°C. However in 1985, they did not come near the coast though sea temperature ranged between 8° and 12°C. Saunders et al. (1975) reported the lethal temperature of salmon in seawater to be −0.7°C. This precludes the possibility of salmon overwintering in the Gulf of St. Lawrence unless they return to freshwater, as do some salmon in the Koksoak River (Côté et al. 1984; Robitaille et al. 1984a, b), or move down to midwater, a behavior described for salmon in the Baltic in response to high temperatures (>12°C) at the surface (Alm 1958). Comeau (1909) reported postsmolts found in the stomach of seals off Pointe-des-Monts in January and February. Low sea temperature has been hypothesized as limiting the passage of Koksoak River smolts (Ungava Bay) to West Greenland in some years, thereby resulting in an estuarine population (Power 1969, 1981). This situation might also be hypothesized to occur in the Gulf of St. Lawrence. For instance in 1983, mean air temperature, not to mention minimal temperature, decreased from 4° to 0°C and less in a short period near the end of October. Masses of seawater carried by gyres east and west of Anticosti Island, and presenting momentarily favorable conditions, can get surrounded by masses of seawater at lower temperature. Should salmon rely on temperature as a cue for their movement out of the Gulf of St. Lawrence, then late migrants could not escape as conditions deteriorate.

The origin of postsmolts collected in this study is not known. They may be a particular subgroup of some north shore stocks. Postsmolts in this study smoltified earlier and at a smaller size than stocks in northern Newfoundland (Chadwick 1981). However, their origin cannot be determined based on smolt length or smolt age distributions. For instance, there is a general tendency for increasing smolt age with latitude, but there is much variability in the data at latitudes below 52°. Data for salmon stocks in rivers near 50° latitude range from 3 to 4 years (Power 1981). Furthermore, postsmolts in this study had an age distribution similar to that of salmon in the Port-aux-Basques (Newfoundland) drift net fishery. Port-aux-Basques salmon migrated to rivers all around the Gulf of St. Lawrence (Belding and Préfontaine 1938).

Postsmolts in this study may also be from a particular subgroup of individuals, such as late-migrant smolts. Power and Shooner (1966) and Randall and Power (1979) observed remnants of the smolt migration feeding in river estuaries on the north shore of the Gulf of St. Lawrence in July and August. Furthermore coho salmon released in mid- to late-summer did not leave the general area of release (Mahnken and Joyner 1973).

Since grilse are known not to migrate as far as 2- and 3-sea-year salmon in the Northwest Atlantic (Ruggles and Ritter 1980), postsmolts in this study can be thought of as potential grilse. However, the only indication in that direction that we have is the observation that some males having a summer check on their scales in 1982 had a higher gonadosomatic index than males having no summer check on their scales (0.042 and 0.025% respectively). However, this is based on a small number of postsmolts as few salmon exhibited a summer check in 1982 and, unfortunately, no gonads were preserved in 1983–85. There are some stocks maturing mainly as grilse among the north shore stocks, but grilse are nearly exclusively males in these stocks (Schiefer 1972; Caron 1984). Postsmolts in this study were 62% females. Female grilse are common in Newfoundland (Chadwick 1981; Power 1981). There are no published data on Anticosti stocks. Poten-

tial grilse have been reported from the Grand Bank in offshore fisheries in the Northwest Atlantic (Reddin 1985), and it has been suggested that stocks maturing as grilse in the Bay of Fundy may not leave the general area throughout their entire marine life (Jessop 1976).

Knowledge on the marine biology of Atlantic salmon postsmolts has been a neglected area of research. Their continual presence in sea surface waters could prove to be extremely valuable in forecasting salmon movements and production (Chadwick 1982; Scarnecchia 1984). Potential studies include mortality rates in the period of transition (July) and the relationship between low temperatures (3°–4°C) and postsmolt migration out of the Gulf of St. Lawrence. Biological data in general are needed to be included in models forecasting salmon runs in the North Atlantic.

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LITERATURE CITED

ALLAN, I. R. H., AND J. A. RITTER.
1977. Salmonid terminology. J. Cons. int. Explor. Mer 37:293–299.

ALLEN, K. R., R. L. SAUNDERS, AND P. F. ELSON.
1972. Marine growth of Atlantic salmon (*Salmo salar*) in the Northwest Atlantic. J. Fish. Res. Board Can. 29:1373–1380.

ALM, G.
1958. Seasonal fluctuations in the catches of salmon in the Baltic. J. Cons. int. Explor. Mer 23:399–433.

ANONYMOUS.
1984. Report of the Baltic salmon and trout working group. ICES C.M. 1984/Assess:11.

BELDING, D. L., AND G. PRÉFONTAINE.
1938. Studies on the Atlantic salmon. II-Report on the salmon of the 1937 Port-aux-Basques (Newfoundland) drift-net fishery. Contrib. Inst. Zool. Univ. Montréal 3, 58 p.

CARLIN, B.
1959. Results of salmon smolt tagging in the Baltic area. Rapp. P.-v. Réun. Cons. int. Explor. Mer 147:89–96.

CARLIN, B., AND H.-E. LUNDIN.
1967. The size and position of the salmon caught in drift nets in the Baltic. Swed. Salmon Res. Inst. Rep. 14, 6 p.

CARON, F.
1983. Migration vers l'Atlantique des post-saumoneaux (*Salmo salar*) du Golfe du Saint-Laurent. Nat. can. (Rev. Ecol. Syst.) 110:223–227.
1984. Rapport d'opération de la rivière Trinité, 1984. Gouvernement du Québec, Ministère du Loisir, de la Chasse et de la Pêche, Direction générale de la faune, 26 p.

CHADWICK, E. M. P.
1981. Biological characteristics of Atlantic salmon smolts in Western Arm Brook, Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. 1024, iv + 45 p.
1982. Dynamics of an Atlantic salmon stock (*Salmo salar*) in a small Newfoundland river. Ph.D Thesis, Memorial Univ. Newfoundland, St. John's, 267 p.

CHRISTENSEN, O.
1968. Report on an experimental fishery with salmon drift-nets. ICES C.M. 1968/B:11.

CHRISTENSEN, O., AND P.-O. LARSSON.
1979. Review of Baltic salmon research. ICES Coop. Res. Rep. 89, 124 p.

CHRISTENSEN O., AND W. H. LEAR.
1980. Distribution and abundance of Atlantic salmon at West Greenland. Rapp. P.-v. Réun. Cons. int. Explor. Mer 176:22–35.

COMEAU, N. A.
1909. Life and sport on the north shore of the lower St. Lawrence and Gulf. Telegraph Printing Company, Quebec.

CÔTÉ, Y., I. BABOS, AND J. A. ROBITAILLE.
1984. Caractéristiques scalimétriques des saumons du Koksoak (Ungava, Québec). Nat. can. (Rev. Ecol. Syst.) 111:401–409.

ELSON, P. F.
1953. Growth and migration of Pollett River salmon. St. Andrews Biol. Stn. Annu. Rep., p. 146–148.
1964. Post-smolt Atlantic salmon in the Bay of Fundy. St. Andrews Biol. Stn. Annu. Rep., E20–E23.

HUNTSMAN, A. G.
1939. Conference on salmon problems. Publ. Am. Assoc. Adv. Sci. 8:86–106.

IKONEN, E., AND H. AUVINEN.
1984. Migration of salmon in the Baltic Sea, based on Finnish tagging experiments. ICES C.M. 1984/M:4.
1985. Migration of salmon post-smolts (*Salmo salar*) in the Baltic Sea. ICES C.M. 1985/M:19.

JESSOP, B. M.
1976. Distribution and timing of tag recoveries from native and nonnative Atlantic salmon (*Salmo salar*) released into Big Salmon River, New Brunswick. J. Fish. Res. Board Can. 33:829–833.

JUTILA, E., AND T. ALAPASSI.
1985. Recaptures of salmon post-smolts (*Salmo salar*) during the first summer after release in Finnish tagging experiments. ICES C.M. 1985/M:28.

JUTILA, E., AND J. TOIVONEN.
1985. Food composition of salmon post-smolts (*Salmo salar*) in the northern part of the Gulf of Bothnia. ICES C.M. 1985/M:21.

KENDALL, W. C.
1935. The fishes of New England, the salmon family. Part 2. The salmons. Mem. Bos. Soc. Nat. Hist. 9:1–166.

KULKA, D. W., S. COREY, AND T. D. ILES.
1982. Community structure and biomass of euphausiids in the Bay of Fundy. Can. J. Fish. Aquat. Sci. 39:326–334.

LABAR, G. W., J. D. MCCLEAVE, AND S. M. FRIED.
1978. Seaward migration of hatchery-reared Atlantic salmon (*Salmo salar*) smolts in the Penobscot River estuary, Maine: open-water movements. J. Cons. int. Explor. Mer 38:257–269.

LARSSON, P.-O.
1974. Migration of the Swedish west coast salmon stocks. Swed. Salmon Res. Inst. Rep. 3, 11 p.
1985. Predation on migrating smolt as a regulating factor in Baltic salmon, *Salmo salar*, populations. J. Fish Biol. 26:391–397.

LARSSON, P.-O., AND S. ATEŠHKAR.
1979. Laxsmoltens vandring fraan Lulealven. Fiskeritidskrift Finl. 1:8–9.

LEAR, W. H.
1972. Food and feeding of Atlantic salmon in coastal areas and over oceanic depths. ICNAF Res. Bull. 9:27–39.
1973. Size and age composition of the 1971 Newfoundland-Labrador commercial salmon catch. Fish. Res. Board Can. Tech. Rep. 392, 43 p.
1980. Food of Atlantic salmon in the West Greenland-Labrador Sea area. Rapp. P.-v. Réun. Cons. int. Explor. Mer 176:55–59.

LEAR, W. H., AND R. K. MISRA.
1978. Clinal variation in scale characters of Atlantic salmon (*Salmo salar*) based on discriminant function analysis. J. Fish. Res. Board Can. 35:43–47.

MAHNKEN, C., AND T. JOYNER.
1973. Salmon for New England fisheries. III: Developing a coastal fishery for Pacific salmon. Mar. Fish. Rev. 35(10):9–13.

MAY, A. W.
1973. Distribution and migrations of salmon in the Northwest Atlantic. Int. Atl. Salmon Found. Spec. Publ. Ser. 4:373–382.

MEISTER, A. L.
1984. The marine migrations of tagged Atlantic salmon (*Salmo salar*) of USA origin. ICES C.M. 1984/M:27.

MUNRO, W. R.
1970. Notes on the salmon long-lining cruise by the R.V. "Jens Chr. Svabo" off Faroe, April 1969. ICNAF Res. Doc. 70/40, 8 p.

MURRAY, A. R.
1968. Smolt survival and adult utilisation of Little Codroy River, Newfoundland, Atlantic salmon. J. Fish. Res. Board Can. 25:2165–2218.

PEPPAR, J. L.
1982. Atlantic salmon smolt investigations, Restigouche River system, New Brunswick. Can. MS Rep. Fish. Aquat. Sci. 1641, vii + 15 p.

POWER, G.
1969. Salmon of Ungava Bay. Arct. Inst. N. Am. Tech. Pap. 22, 72 p.
1981. Stock characteristics and catches of Atlantic salmon (*Salmo salar*) in Quebec, and Newfoundland, and Labrador in relation to environmental variables. Can. J. Fish. Aquat. Sci. 38:1601–1611.

POWER, G., AND G. SHOONER.
1966. Juvenile salmon in the estuary and lower Nabisipi River and some results of tagging. J. Fish. Res. Board Can. 23:947–961.

RANDALL, R. G., AND G. POWER.
1979. Atlantic salmon (*Salmo salar*) of the Pigou and Bouleau Rivers, Quebec. Environ. Biol. Fish. 4:179–184.

REDDIN, D. G.
1985. Atlantic salmon (*Salmo salar*) on and east of the Grand Bank. J. Northwest Atl. Fish. Sci. 6:157–164.

REDDIN, D. G., AND J. E. CARSCADDEN.
1981. Salmon-capelin interactions. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 81/2, 38 p.

ROBITAILLE, J. A., Y. COTE, G. HAYEUR, AND G. SHOONER.
1984a. Particularités de la reproduction du saumon atlantique (*Salmo salar*) dans une partie du reseau Koksoak, en Ungava. Rapp. tech. can. sci. halieut. aquat. 1313, vii + 33 p.
1984b. Croisssance estuarienne du saumon atlantique (*Salmo salar*) dans le fleuve Koksoak, en Ungava. Rapp. tech. can. sci. halieut. aquat. 1314, vii + 23 p.

RUGGLES, C. P., AND J. A. RITTER.
1980. Review of North American smolt tagging to assess the Atlantic salmon fishery off West Greenland. Rapp. P.-v. Réun. Cons. int. Explor. Mer 176:82–92.

SAUNDERS, R. L.
1966. Some biological aspects of the Greenland salmon fishery. Atl. Salmon J., Summer:17–23.
1986. The thermal biology of Atlantic salmon: influence of temperature on salmon culture with particular reference to constraints imposed by low temperature. Inst. Freshwater Res. Drottningholm Rep. 63, 38 p.

SAUNDERS, R. L., B. C. MUISE, AND E. B. HENDERSON.
1975. Mortality of salmonids cultured at low temperature in seawater. Aquaculture 5:243–252.

SCARNECCHIA, D. L.
1983. Age at sexual maturity in Icelandic stocks of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 40:1456–1468.
1984. Climatic and oceanic variations affecting yield of Icelandic stocks of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 41:917–935.

SCHIEFER, K.
1972. Ecology of Atlantic salmon, with special reference to occurrence and abundance of grilse, in north shore Gulf of St. Lawrence rivers. Ph.D Thesis, Univ. Waterloo, Ontario, 129 p.

SIEGEL, S.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., N.Y., 312 p.

SNEDECOR, G. W., AND W. G. COCHRAN.
1967. Statistical methods. Iowa State Univ. Press, Ames, IO, 593 p.

SOIKKELI, M.
1973. Tagged salmon smolts in the diet of the Caspian tern. Laxforskningsinst. Medd. 3:1–5.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. The principles and practice of statistics in biological research. Freeman and Co., San Francisco, CA., 776 p.

TEMPLEMAN, W.
1967. Atlantic salmon from the Labrador Sea and off West Greenland, taken during A. T. Cameron cruise, July–August 1965. ICNAF Res. Bull. 4:5–40.
1968. Distribution and characteristics of Atlantic salmon over oceanic depths and on the bank and shelf slope areas off Newfoundland, March–May 1966. ICNAF Res. Bull. 5:62–85.

THUROW, F.
1968. On food, behavior and population mechanisms of Baltic salmon. Swed. Salmon Res. Inst. Rep. 4, 16 p.

VALLE, E.
1985. Predation of birds on salmon and sea trout smolts and post-smolts. ICES C.M. 1985/M:22.

VIBERT, R.
1953. Voyages maritimes des saumons et retour à la rivière natale. Bull. Fr. Piscic. 170:5–23.

SIZE AND DIET OF JUVENILE PACIFIC SALMON DURING SEAWARD MIGRATION THROUGH A SMALL ESTUARY IN SOUTHEASTERN ALASKA

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ABSTRACT

To assess competition and predation among juvenile Pacific salmon (*Oncorhynchus* spp.) migrating through the estuary of Porcupine Creek, a small stream in southeastern Alaska, their size and diet were determined in 1979 and 1981. Mean fork length (FL) during May and June increased from 32 to 73 mm (1.5 mm/day) for pink salmon, *O. gorbuscha*; from 39 to 51 mm (0.4 mm/day) for chum salmon, *O. keta*; and during June and July, from 99 to 165 mm (1.6 mm/day) for coho salmon, *O. kisutch*. Prey, in order of importance, included larval fish (mostly Gadidae), larval molluscs (Mesogastropoda), and calanoid copepods for pink salmon; larval molluscs, larvaceans, and hyperiid amphipods for chum salmon; and fish (*Clupea harengus pallasi*, *Ammodytes hexapterus*, and Gadidae), insects, and larval decapods (Brachyrhyncha) for coho salmon. No pink or chum salmon were found in the coho salmon stomachs. Prey size for pink and chum salmon was similar (median, 0.4 mm long for both species), and much smaller than that of coho salmon (median, 2.3 mm). Diet overlap was greater between pink and chum salmon than between either species and coho salmon. Pink salmon, however, ate almost exclusively (95%) pelagic prey, whereas chum salmon ate both pelagic (74%) and epibenthic (26%) prey. Rapid early growth and differences in diet probably help minimize predation and competition among salmon during seaward migration.

The early marine life stage of juvenile Pacific salmon (*Oncorhynchus* spp.), during transition from freshwater to seawater, is important in determining brood-year survival and subsequent adult returns (Manzer and Shepard 1962; Parker 1968); their survival rate is lowest during this time (Parker 1968; Bax 1983). Salmon often school in large concentrations in estuaries as they migrate seaward, and are more likely to deplete food supplies and compete for food than after they disperse to the sea (Bailey et al. 1975; Feller and Kaczynski 1975). Survival depends on size (Parker 1971; Healey 1982), and competition for food can depress early growth (Peterman 1984) and prolong vulnerability to predators (Taylor 1977; Walters et al. 1978). Size and diet of juvenile salmon in an estuary, therefore, determine the potential for predation and competition and can greatly affect survival.

As salmon aquaculture expands and more juvenile salmon are released into estuaries, competition and predation among salmon may increase (Johnson 1974). To optimize hatchery production and avoid adversely affecting wild stocks, an understanding is needed of how different stocks of salmon interact in estuaries. This paper compares size and diet of juvenile pink, *O. gorbuscha*; chum, *O. keta*; and coho, *O. kisutch*, salmon to assess potential predation and competition between the species during their seaward migration through the estuary of a small, pristine stream.

STUDY AREA

This study was conducted in the estuary of Porcupine Creek, the only salmon stream flowing into Steamer Bay in southeastern Alaska (Fig. 1). The estuary (about 5.5 km long) consists of a 1.5 km stream reach that is periodically inundated by tides, and a 4 km series of three estuarine basins. At low tide, the inner and middle basins are small (2 and 7 ha, respectively) and shallow (14 and 16 m, respectively) compared with the outer basin (120 ha and 42 m deep). The littoral zone ranges from low-gradient mudflats to steep cobble. Bottoms of the basins are level and composed of shell, gravel, and mud.

During low tide, the inner and middle basins are partially isolated from the outer basin and the main part of Steamer Bay by tidal rapids 1–3 m deep. Salinity is lower in the inner and middle

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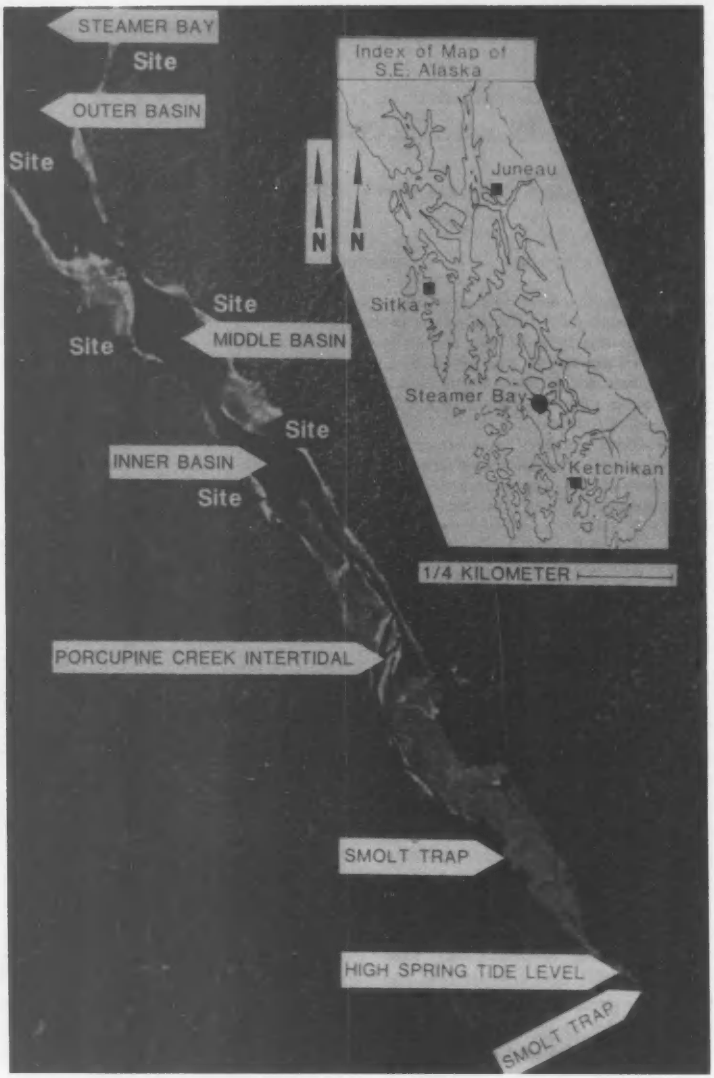

FIGURE 1.—Aerial photo of study site in the inner part of Steamer Bay, southeastern Alaska, showing the Porcupine Creek estuary at low tide and location of smolt traps used by Thedinga (1985).

basins (24–29‰) than in the outer basin (28–30‰), but temperature does not differ between basins in spring and summer (11°–13°C from May to September 1981). Heavy tidal flushing, particularly during spring tides, results in a diverse community within the estuary; e.g., eel grass, *Zostera*; Dungeness crabs, *Cancer magister*; bull kelp, *Nereocystis*; and rock scallop, *Hinnetes*. A detailed description of the study area is in Merrell and Koski (1978) and Koski (1984).

Porcupine Creek, upstream of tidal influence, is 4.5 km long and has an average discharge of

about 0.5 m^3/second. Its watershed is forested by mature western hemlock, *Tsuga heterophylla*, and Sitka spruce, *Picea sitchensis*. Annually, 5,000–75,000 adult pink salmon and 200–4,000 chum salmon spawn in the creek from late July to October, and 250–600 adult coho salmon spawn from late September to November (Koski 1984). Pink and chum salmon fry typically migrate from Porcupine Creek from late March to mid-May (Koski[2]). Coho salmon smolts migrate from late April to early June, but over 90% usually migrate in late May (Thedinga 1985).

METHODS

Six stations, one each on the east and west sides of the three basins (Fig. 1) were sampled by a beach seine 37 m long, with 1.6 cm stretch mesh on the wings, and a central bag of 6 mm stretch mesh. The seine tapered from 2 m deep at the central bag to 1 m deep at each end. In 1979, only one station in each basin was seined about every 4 days from 16 May to 12 June. In 1981, all six stations were seined biweekly from 26 May to 7 July and monthly thereafter through 11 November. Seines were set parallel to and about 40 m from shore by a skiff, and retrieved from shore. Setting and retrieval were accomplished within 10 minutes.

All fish caught were identified and counted. Fork lengths (FL) were measured to the nearest millimeter from a random sample of ≤25 salmon per species, station, and sampling period. Stomach contents were collected only in 1981 from ≤10 salmon per species and station in May, June, and July. Contents were collected from anesthetized fish by flushing the stomach with water from a syringe (Meehan and Miller 1978; Koski and Kirchhofer 1984) and preserved in 5% formaldehyde. Prey were later identified, counted, measured, and weighed.

For diet analysis, the index of relative importance (IRI) was calculated, where

IRI = (% number + % weight) (% frequency of occurrence)

(Pinkas et al. 1971). Diet overlap between salmon species was calculated (McCabe et al. 1983):

$$C = \frac{2\sum_{i=1}^{s} X_i Y_i}{\left(\sum_{i=1}^{s} X_i^2 + \sum_{i=1}^{s} Y_i^2\right)}$$

where C = overlap coefficient and X_i and Y_i are proportions of the total diet of salmon species X and Y, respectively, contributed by prey taxon i of s prey taxa. Diet overlap was calculated separately for proportions based on prey number and weight. Prey were also classified as epibenthic or pelagic to assess overlap in foraging mode (Feller and Kaczynski 1975). Epibenthic prey were polychaetes, gammarid amphipods, harpacticoid copepods, barnacle cyprids, and cumaceans. Pelagic prey were calanoid copepods, euphausiids, barnacle nauplii, cladocerans, larvaceans, larval decapods (Brachyrhyncha), hyperiid amphipods, and fish (eggs, larvae, and juveniles).

RESULTS

Size

In May 1979, pink salmon were the size of newly emergent fry, about 32 mm FL (Fig. 2). Average length increased 1.5 mm/day, to 73 mm on 12 June 1979. In 1981, pink salmon averaged 73 mm FL in late May and early June. Changes in average FL in 1981 could not be calculated because most migration occurred before sampling began.

Average FL of chum salmon increased slower than that of pink salmon. Mean FL of chum salmon increased 0.4 mm/day in both years, from 39 mm to 51 mm in 1979, and from 60 mm to 78 mm in 1981 (Fig. 2). Chum salmon averaged about 10 mm FL longer in 1981 than in the same period in 1979. Chum salmon were not found in the estuary after early July, except for two fry caught in the outer basin in November.

Average FL of coho salmon was nearly constant, between 85 and 110 mm, throughout May and early June in both 1979 and 1981 (Fig. 2). Average FL of coho salmon in the estuary during this period was influenced by an influx of Porcupine Creek migrants, which averaged between 75 and 96 mm FL (Thedinga 1985). After the migration from Porcupine Creek in 1981 (≈9 June), average FL increased 1.6 mm/day to 165 mm by 20 July. Average FL then decreased to 85 mm in

[2]K. V. Koski, Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 210155, Auke Bay, AK 99821, pers. commun. October 1985.

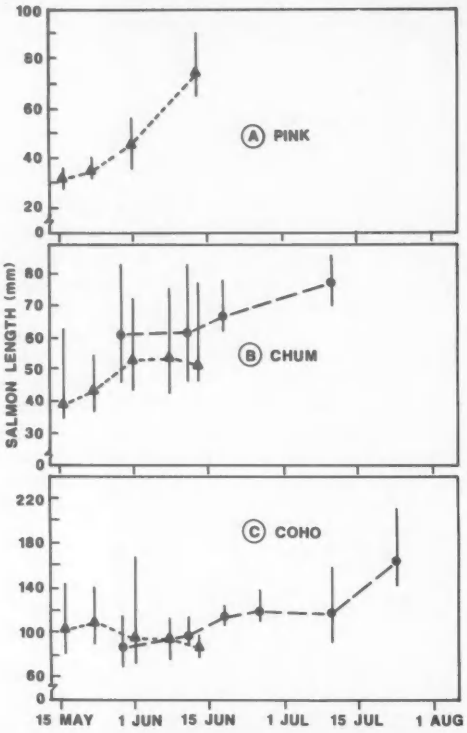

FIGURE 2.—Length of salmon in 1979 and 1981. Data shown are means and ranges for pooled samples from all stations on each sampling date. Data for pink salmon in 1981 are omitted because of small sample sizes. (▲ = 1979, ● = 1981.)

August and 106 mm in September, after most smolts had left and a few new smolts entered the estuary.

Diet

A wide variety of prey was eaten by the three salmon species, but usually only one or two prey taxa dominated the diet (Table 1). Pink salmon ate mostly larval molluscs (Mesogastropoda) and larval fish (mostly Gadidae) in May, and calanoid copepods in June. Chum salmon ate mostly larval molluscs in May; larval molluscs, larvaceans, and cladocerans in June; and hyperiid amphipods and larval decapods in July. Coho salmon ate mostly fish and insects in May and June, and fish and larval decapods in July. The identifiable fish prey of coho salmon consisted of 53% Pacific herring, *Clupea harengus pallasi*; 45% cod (Gadidae); and 2% Pacific sand lance, *Ammodytes hexapterus*. No identifiable pink or chum salmon were in the coho stomachs. Catch of coho, but not that of the other salmon, was significantly correlated ($r = 0.46$, $P < 0.001$) with aggregate catch of herring, sand lance, and cod, indicating that coho salmon congregated near prey schools.

Diet overlap was higher between pink and chum salmon than between either species and coho salmon (Table 2). Diet overlap between pink and chum salmon was especially high in May when both species ate large numbers of larval molluscs. If based on prey weight, diet overlap between pink and coho salmon was negligible. If based on prey number, however, overlap was >50% in June when both pink and coho salmon ate large numbers of calanoid copepods. Diet overlap between chum and coho salmon was consistently low, especially when based on prey weight.

Of the 12 most important prey taxa in May and June, when all 3 salmon species were present in the estuary, only 4 differed significantly ($P < 0.05$) in mean number per stomach between pink and chum salmon, whereas 9–10 differed significantly between the two species and coho salmon (Table 3). Compared with pink salmon, chum salmon ate more harpacticoid copepods, cladocerans, and insects. Coho salmon ate fewer small plankton and more fish than did the other salmon species. Coho salmon averaged fewer than 20 total prey items, compared to more than 100 in pink salmon and 200 in chum salmon.

Coho salmon ate larger prey than did the other salmon (Fig. 3). Median prey length for coho salmon was 2.3 mm, compared with 0.4 mm for pink and chum salmon. Coho salmon generally selected larger individuals of each prey taxon—particularly larger calanoid copepods, gammarid amphipods, euphausiids, and larval decapods—than did pink and chum salmon (Table 4). Of fish prey, coho salmon ate mostly juveniles, whereas pink and chum salmon ate mostly eggs and larvae.

As they grew larger, all three salmon species selected larger prey. Numbers of hyperiid amphipods, euphausiids, and fish larvae—all relatively large prey—were positively correlated with FL of pink or chum salmon, whereas numbers of cladocerans and larvaceans—both relatively small prey—were negatively correlated with chum salmon FL (Table 5). Numbers of calanoid copepods and fish were positively correlated with coho salmon FL, whereas the number

TABLE 1.—Stomach contents of juvenile salmon in Porcupine Creek estuary, 26 May–7 July 1981. %*N* is percent by number, %W is percent by wet weight, %FO is percent frequency of occurrence of fish with prey item *i*, and %IRI is percent of total sum of IRI for all prey taxa. IRI = (%*N* + %*W*)%FO. Taxa are omitted if %IRI is ≤3 for all salmon species.

Prey taxon	Pink salmon				Chum salmon				Coho salmon			
	%*N*	%*W*	%FO	%IRI	%*N*	%*W*	%FO	%IRI	%*N*	%*W*	%FO	%IRI
26–29 May 1981												
Mollusc larvae	47	2	71	28	59	36	100	60	2	0	4	0
Calanoida	12	2	57	7	5	4	71	5	0	0	4	0
Harpacticoida	1	0	29	0	11	9	90	12	17	1	18	3
Cladocera	1	0	43	1	14	5	77	10	0	0	4	0
Cumacea	0	0	0	0	2	9	32	3	16	1	41	6
Euphausiacea	11	2	71	8	0	2	42	1	0	0	0	0
Decapod larvae												
Shrimp	9	5	71	8	0	1	13	0	0	0	0	0
Crabs	8	2	60	4	3	3	60	2	2	0	12	0
Fish eggs and larvae	8	86	57	44	0	21	13	2	1	6	4	0
Fish	0	0	0	0	0	0	0	0	22	62	48	38
Insects[1]	1	0	29	0	1	5	52	2	29	23	100	47
Total	98	99		100	95	95		97	89	93		94
(Number of stomachs)			(7)				(31)				(27)	
9–10 June 1981												
Mollusc larvae	9	5	100	8	24	16	73	23	0	0	7	0
Calanoida	47	52	100	58	5	5	65	5	22	0	43	9
Harpacticoida	3	5	25	1	4	4	65	4	0	0	7	0
Cladocera	13	7	75	9	19	8	81	17	1	0	23	0
Decapod larvae												
Shrimp	1	1	75	1	0	1	20	0	0	0	0	0
Crabs	4	11	100	5	7	12	100	8	19	0	21	4
Larvacea, Oikopleura	9	5	100	8	20	13	85	23	7	0	14	1
Fish eggs and larvae	6	5	100	6	11	12	35	6	0	0	0	0
Fish juveniles	0	0	0	0	0	0	0	0	10	94	71	70
Insects[1]	0	1	50	0	3	10	75	8	28	2	50	14
Total	92	92		96	93	91		94	87	96		98
(Number of stomachs)			(4)				(26)				(14)	
7 July 1981												
Calanoida	—	—	—	—	4	1	43	3	16	0	24	5
Hyperiidea	—	—	—	—	12	30	88	45	4	0	29	2
Decapod larvae												
Shrimp	—	—	—	—	61	40	14	18	1	0	6	0
Crabs	—	—	—	—	3	10	86	9	55	5	53	25
Fish eggs and larvae	—	—	—	—	0	3	57	2	0	0	0	0
Fish juveniles	—	—	—	—	0	0	0	0	9	94	50	65
Insects[1]	—	—	—	—	6	4	100	14	5	0	24	2
Total	—	—	—	—	86	88		91	90	99		99
(Number of stomachs)			(0)				(7)				(17)	

[1]Mostly adult Diptera.

of insects was negatively correlated. As a consequence of the selection of larger prey as the salmon grew, total prey weight increased with salmon FL, whereas total prey number did not (Table 5). Although pink and chum salmon ate prey of similar size, they foraged differently (Fig. 4). Pink salmon consumed about 95% pelagic prey; chum salmon, only 74%. Individual taxa changed, but the importance of pelagic prey did not change significantly between sampling periods, estuary basins, or salmon FL classes.

Diet of coho salmon, on the other hand, varied widely depending on salmon FL, date, and location (Fig. 4). Pelagic prey increased from 1% of total prey for coho salmon <80 mm FL to 80% for those >100 mm FL. Coho salmon ate fewer pelagic prey in May, when most coho were in the inner basin and feeding mainly on insects, than in July when most were in the outer basin and feeding mainly on fish (Table 1). Analysis of variance, however, showed that differences between basins and sampling periods were not significant

TABLE 2.—Diet overlap (McCabe et al. 1983) based on number (*n*) and weight (*W*) of prey by sampling period for juvenile salmon in Porcupine Creek estuary, 26 May–7 July 1981. The number of stomach samples is in Table 1.

Sampling period	Pink vs. chum		Pink vs. coho		Chum vs. coho	
	n	*W*	*n*	*W*	*n*	*W*
26–29 May	0.87	0.40	0.07	0.09	0.13	0.08
9–10 June	0.47	0.38	0.54	0.00	0.29	0.00
7 July	—	—	—	—	0.10	0.01

TABLE 3.—Comparison of mean number of the 12 most important prey and total of all prey per salmon stomach from Porcupine Creek estuary, 26 May–10 June 1981. Means followed by the same letter are not significantly different (Kruskal-Wallis analysis of variance, $P>0.05$) compared within a row and across columns. The number of stomach samples is in Table 1.

Prey item	Pink salmon	Chum salmon	Coho salmon
Mollusc larvae	28 a	86 a	0 b
Barnacle larvae	4 a	5 a	0 b
Calanoida	40 a	12 b	0 b
Harpacticoida	2 a	19 b	3 a
Cladocera	10 a	37 b	0 c
Cumacea	0 a	5 a	2 a
Euphausiacea	5 a	1 a	0 b
Decapod larvae	11 a	12 a	0 b
Larvacea	6 a	20 a	0 b
Fish eggs and larvae	3 a	11 a	0 b
Fish	0 a	0 a	4 b
Insects	0 a	4 b	6 b
Total	115 a	216 a	19 b

TABLE 4.—Mean length (mm) of prey items in salmon stomachs from Porcupine Creek estuary, 26 May–7 July 1981. Mean prey length within prey taxa was significantly greater for coho salmon than for pink or chum salmon (sign test, $n=12$ means, $P=0.03$ and $P=0.003$, for coho salmon vs. pink and chum salmon, respectively). The number of stomach samples is in Table 1.

Prey item	Pink salmon	Chum salmon	Coho salmon
Mollusc larvae	0.5	0.5	0.4
Barnacle larvae	0.4	0.7	0.4
Calanoida	1.2	1.2	4.8
Harpacticoida	1.3	1.1	1.3
Cladocera	0.6	0.6	0.7
Cumacea	2.4	2.5	2.8
Hyperiidea	3.3	2.4	3.0
Gammaridea	1.5	1.8	5.2
Euphausiacea	3.5	3.0	18.0
Decapod larvae	2.8	2.0	3.5
Larvacea	0.8	0.9	—[1]
Fish, all life stages	2.0	1.2	23.9
Insects	2.8	2.2	3.5

[1]None present.

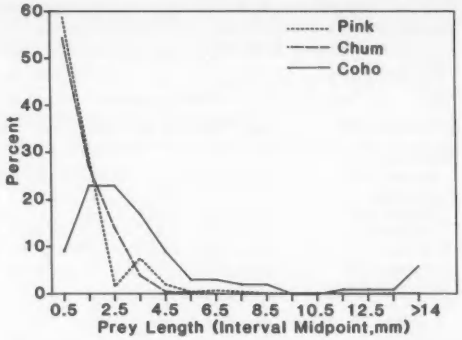

FIGURE 3.—Relative frequencies of length of prey eaten by pink, chum, and coho salmon in the Porcupine Creek estuary in 1981. Total prey measured were 687 in 11 pink, 5,634 in 63 chum, and 1,179 in 53 coho salmon.

TABLE 5.—Spearman rank correlations between number of prey items and fork length of juvenile salmon. Because of the large number of correlations tested, significance levels were adjusted by multiplying the probability *P* by the number of tests for each salmon species. The number of stomach samples is in Table 1.

Prey item	Pink salmon	Chum salmon	Coho salmon
Mollusc larvae	−0.32	0.05	−0.18
Barnacle larvae	−0.36	−0.02	0.22
Calanoida	−0.51	0.10	0.33*
Harpacticoida	−0.30	−0.03	−0.19
Cladocera	−0.06	−0.34*	−0.04
Cumacea	−0.20	0.04	−0.28
Hyperiidea	−0.35	−0.37*	0.19
Euphausiacea	0.84*	0.36*	0.15
Decapod larvae	0.43	−0.19	0.25
Larvacea	−0.36	−0.50*	—[1]
Fish eggs	−0.33	−0.18	—[1]
Fish larvae and juveniles	0.86*	−0.04	0.36*
Insects	0.61	−0.11	−0.71**
Total prey number	−0.40	−0.04	−0.09
Total prey weight	0.85*	0.35*	0.66**

[1]None present in any stomachs.
*Adjusted probability $P < 0.05$.
**Adjusted probability $P < 0.01$.

after adjusting for differences in coho salmon FL (Table 6). Thus, changes in diet were mainly related to increasing size of coho salmon as they migrated through the estuary.

DISCUSSION

Both size and diet can affect predation and competition among juvenile salmon in an estuary. A

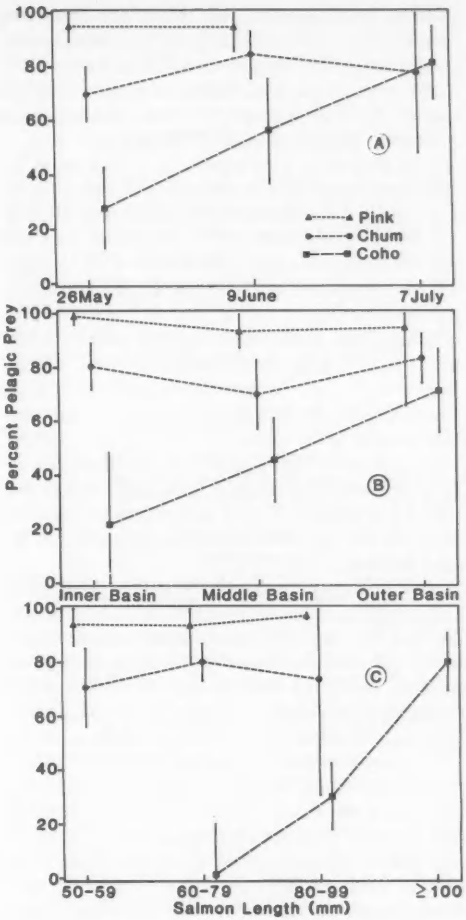

FIGURE 4.—Number of pelagic prey as percent of total prey eaten by individual salmon compared between sampling periods (A), estuary basins (B), and salmon fork length classes (C) in the Porcupine Creek estuary in 1981. Symbols are means; bars are ±2 SE of the means. Symbols in *B* and *C* are the same as in *A*. Pelagic prey are defined in the text.

TABLE 6.—Analysis of variance of percentage pelagic prey of coho salmon, with sampling period and estuary basin as factors and salmon fork length as covariate. Factors, covariate, and interactions were adjusted simultaneously before assessing significant (Kim and Kohout 1975).

Source of variation	df	Mean square	*F*	*P*
Length	1	8,458	9.4	0.004
Sampling period	2	1,580	1.8	0.184
Basin	2	654	0.7	0.489
Residual	47	900	—	—
Total	52	1,519	—	—

salmon's size mainly influences its vulnerability to predators, whereas its diet determines potential competition for food. Size and diet, however, are not independent. Salmon change their diet as they grow, which helps relieve competition between salmon of different size, and a poor diet slows their growth, which prolongs vulnerability to predation.

Because of similar diets, pink and chum salmon are potential competitors. Although diets of pink and chum salmon in the Porcupine Creek estuary were similar in prey size and some prey taxa, however, pink salmon fed almost solely on pelagic prey , whereas chum salmon foraged both pelagically and epibenthically; such differences may help reduce competition. Competition probably also was reduced because, as the salmon grew larger, they switched to larger prey. Coho salmon probably did not compete for food with the other two species because the coho fed on larger, different prey.

Rapid early growth of salmon is important in reducing vulnerability to predators (Parker 1971; Taylor 1977). For example, hatchery pink salmon fry raised for 60 days (to 40 mm FL) before release into an estuary in southeastern Alaska survived 68% better at sea than did fry released immediately after emergence (Martin et al. 1981). Marine survival also is higher for year classes of larger (9–11 cm FL) than for smaller (6–8 cm FL) sockeye salmon, *O. nerka*, smolts (Foerster 1954). Coho salmon smolts from Porcupine Creek in 1978 averaged 99 mm FL and their survival was twice that of the 1979 smolts, which averaged only 91 mm FL (Thedinga 1985). Smolt size and migration timing, however, interact complexly to influence marine survival of coho salmon (Bilton 1978).

Growth of juvenile salmon in estuaries usually is inferred from changes in mean size (LeBrasseur and Parker 1964; Healey 1978), but these estimates are subject to bias. In this study, changes in mean size of fish in the catches on successive dates could underestimate real growth for two reasons: 1) small individuals may have migrated continuously into the estuary from

freshwater and 2) larger individuals may have migrated continuously from the estuary to the sea. Conversely, growth could be overestimated if predators of salmon selected small individuals (Parker 1971). In addition, although the inner and middle basins are semiisolated from adjacent marine waters during low tide, juvenile salmon from adjacent waters could easily enter the estuary, especially the outer basin, during flood tide and mix with salmon from Porcupine Creek.

Estimates of salmon growth in estuaries and nearshore marine waters are variable, but generally range between 1 and 2 mm/day. LeBrasseur and Parker (1964) estimated pink salmon growth to be 0.9 mm/day during the first 30 days at sea, and Healey (1978) estimated pink salmon growth during summer to be 1.0 mm/day; our estimate was 1.5 mm/day. Our estimate for chum salmon at 0.4 mm/day was considerably less than that of Healey (1978) at 1.5 mm/day, also based on change in mean length; however, our estimate for coho salmon of 1.6 mm/day was similar to that of Healey (1978) at 1.2 mm/day. Summer growth back-calculated from scales of salmon from the Sea of Okhotsk was about 1.6 mm/day for pink and chum salmon (Birman 1969).

Because of their initial small size, pink and chum salmon particularly are vulnerable to predators including juvenile coho salmon (Parker 1971). Several authors have suggested that a major share of pink salmon mortality in the first weeks at sea results from juvenile coho salmon predation (Parker 1971; Kaczynski et al. 1973; Hargreaves and LeBrasseur 1985), but such predation has not been found in field collections. Parker (1971) demonstrated predation by juvenile coho salmon on pink salmon fry in the laboratory, and juvenile coho salmon are known predators of salmon fry in freshwater (Hunter 1959; Koski and Kirchhofer 1984). However, we have not found any published data that show predation by juvenile coho salmon on other salmon in estuaries or marine waters. Predation by juvenile coho salmon on pink salmon fry migrating from freshwater does occur in the tidal-influenced reach of Porcupine Creek (Koski and Kirchhofer 1984), but such predation apparently does not extend into the estuarine basins. Many fishes have been identified as predators of pink and chum salmon in estuaries, including Pacific herring (Thorsteinson 1960), sea-run cutthroat trout, *Salmo clarki*; cod, *Gadus macrocephalus*; and sculpin, *Leptocottus armatus*, (Bax et al. 1977). We speculate that predation by coho salmon on salmon fry may occur only under circumstances in which the coho salmon are combined with small fry as they migrate from freshwater.

The period of vulnerability of pink and chum salmon fry to predation by juvenile coho salmon is probably relatively short. Within the first 3 weeks after entering the estuary, pink salmon fry can grow larger than the prey fish of juvenile coho salmon. In the laboratory, juvenile coho salmon ate the smallest pink salmon available and did not eat any larger than about 50 mm FL (Parker 1971), which coincides with the largest fish eaten by coho salmon in our study. At a growth of 1 mm/day, pink salmon entering the estuary at 32 mm FL will outgrow predation by coho salmon smolts in 18 days. In Porcupine Creek, most pink and chum salmon migrated from the stream several weeks before coho salmon, which enables them to grow large enough to avoid predation by coho salmon in the estuary. Thus, early migration and rapid growth of pink and chum salmon fry probably are important in reducing predation by coho salmon.

In the Porcupine Creek estuary, competition and predation probably were slight. Competition for food was minimal, as evidenced by the rapid salmon growth, because of differences in prey and foraging mode and because regular tidal flushing probably replenished food supplies, as in Traitors Cove, AK (Bailey et al. 1975). Natural stocking levels in the estuary also probably were below thresholds where competition for food would depress survival. Predation by coho salmon on pink and chum salmon was avoided because the pink and chum salmon migrated earlier than coho salmon and rapidly grew too large for the coho to handle. Thus, in this natural system, competition and predation probably were unimportant because of moderate stocking levels, rapid growth, and differences in diet and timing of migrations. In systems with hatchery inputs, however, stocking levels would probably be higher and salmon size and timing of migrations different than in natural systems, which could increase competition and predation.

Stocking levels and timing of hatchery releases of juvenile salmon in estuaries are important in minimizing competition and predation (Myers 1980). Hatchery releases should avoid combining large concentrations of pink and chum salmon fry so as not to deplete food supplies. Conversely, releases during low predator abundance and good growing conditions—high food availability and warm temperature—could increase growth and

survival. Early releases of coho salmon could increase predation on pink and chum fry (Johnson 1974), especially fry <50 mm FL, if the releases coincide with fry migrations through the estuary.

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LITERATURE CITED

BAILY, J. E., B. L. WING, AND C. R. MATTSON.
1975. Zooplankton abundance and feeding habits of fry of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *Oncorhynchus keta*, in Traitors Cove, Alaska, with speculations on the carrying capacity of the area. Fish. Bull., U.S. 73:846–861.

BAX, N. J.
1983. Early marine mortality of marked juvenile chum salmon (*Oncorhynchus keta*) released into Hood Canal, Puget Sound, Washington, in 1980. Can. J. Fish. Aquat. Sci. 40:426–435.

BAX, N. J., E. O. SALO, B. P. SNYDER, C. A. SIMENSTAD, AND W. J. KINNEY.
1977. Salmon outmigration studies in Hood Canal: a summary—1977. *In* W. J. McNeil and D. C. Himsworth (editors), Salmonid ecosystems of the North Pacific, p. 171–201. Oregon State Univ. Press, Oregon State Univ. Sea Grant Program, Corvallis.

BILTON, H. T.
1978. Returns of adult coho salmon in relation to mean size and time at release of juveniles. Fish. Mar. Serv. Tech. Rep. 832, 73 p. Dep. Fish. Environ., Pac. Biol. Stn., Nanaimo, B.C.

BIRMAN, I. B.
1969. Distribution and growth of young Pacific salmon of the genus *Oncoryhynchus* in the sea. Probl. Ichthyol. 9:651–666.

FELLER, R. J., AND V. W. KACZYNSKI.
1975. Size selective predation by juvenile chum salmon (*Oncorhynchus keta*) on epibenthic prey in Puget Sound. J. Fish. Res. Board Can. 32:1419–1429.

FOERSTER, R. E.
1954. On the relation of adult sockeye salmon (*Oncorhynchus nerka*) returns to known smolt seaward migrations. J. Fish. Res. Board Can. 11:339–350.

HARGREAVES, N. B., AND R. J. LEBASSEUR.
1985. Species selective predation on juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) by coho salmon. (*O. kisutch*). Can. J. Fish. Aquat. Sci. 42:659–668.

HEALEY, M. C.
1978. The distribution, abundance, and feeding habits of juvenile Pacific salmon in Georgia Strait, British Columbia. Fish. Mar. Serv. Tech. Rep. 788, 49 p. Dep. Fish. Environ., Pac. Biol. Stn., Nanaimo, B.C.
1982. Timing and relative intensity of size-selective mortality of juvenile chum salmon (*Oncorhynchus keta*) during early sea life. Can. J. Fish. Aquat. Sci. 39:952–957.

HUNTER, J. G.
1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16:835–886.

JOHNSON, R. C.
1974. Effects of hatchery coho on native Puget Sound stocks of chum salmon fry. *In* D. R. Harding (editor), Proceedings of the 1974 Northeast Pacific Pink and Chum Salmon Workshop, p. 102–109. Dep. Environ., Fish. Vancouver, B.C.

KACZYNSKI, V. W., R. J. FELLER, J. CLAYTON, AND R. J. GERKE.
1973. Trophic analysis of juvenile pink and chum salmon (*Oncorhynchus gorbuscha* and *O. keta*) in Puget Sound. J. Fish. Res. Board Can. 30:1003–1008.

KIM, J. O., AND F. J. KOHOUT.
1975. Analysis of variance and covariance: subprogram ANOVA. 2d ed. *In* N. H. Nie, C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Brent (editors), Statistical package for the social sciences, p. 398–433. McGraw-Hill, N.Y.

KOSKI, K V.
1984. A stream ecosystem in an old-growth forest in southeast Alaska: Part I. Description and characteristics of Porcupine Creek, Etolin Island. *In* W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley (editors), Fish and wildlife relationships in old-growth forests, Proceedings, p. 47–55. Am. Inst. Fish. Res. Biol., Juneau, AK. Available from J. W. Reintjes, Rt. 4, Box 85, Morehead City, NC 28557.

KOSKI, K V., AND D. A. KIRCHHOFER.
1984. A stream ecosystem in an old-growth forest in southeast Alaska. Part IV: Food of juvenile coho salmon, *Oncorhynchus kisutch* in relation to abundance of drift and benthos. *In* W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley (editors), Fish and wildlife relationships in old-growth forests, Proceedings, p. 81–87. Am. Inst. Fish. Res. Biol., Juneau, AK. Available from J. W. Reintjes, Rt. 4, Box 85, Morehead City, NC 28557.

LEBRASSEUR, R. J., AND R. R. PARKER.
1964. Growth rate of central British Columbia pink salmon (*Oncorhynchus gorbuscha*). J. Fish. Res. Board Can. 21:1101–1128.

MANZER, J. I., AND M. P. SHEPARD.
1962. Marine survival, distribution and migration of pink salmon (*Oncorhynchus gorbuscha*) off the British Columbia coast. H. R. MacMillan Lectures in Fisheries, p. 113–122. Symposium on Pink Salmon 1960, Univ. British Columbia, Vancouver.

MARTIN, R. M., W. R. HEARD, AND A. C. WERTHEIMER.
1981. Short-term rearing of pink salmon (*Oncorhynchus gorbuscha*) fry: effect on survival and biomass of returning adults. Can. J. Fish. Aquat. Sci. 38:554–558.

MCCABE, G. T., JR., W. D. MUIR, R. L. EMMETT, AND J. T. DURKIN.
1983. Interrelationships between juvenile salmonids and nonsalmonid fish in the Columbia River estuary. Fish. Bull., U.S. 81:815–826.

MEEHAN, W. R., AND R. A. MILLER.
1978. Stomach flushing: effectiveness and influence on survival and condition of juvenile salmonids. J. Fish. Res. Board Can. 35:1359–1363.

MERRELL, T. R., JR., AND K. V. KOSKI.
1978. Habitat values of coastal wetlands for Pacific coast salmonids. *In* P. E. Greeson, J. R. Clark, and J. E. Clark (editors), Wetland functions and values: the state of our understanding, p. 256–266. Proceedings of the National Symposium on Wetlands, American Water Resource Association, Minneapolis, MN.

MYERS, K. W. W.
1980. An investigation of the utilization of four study areas in Yaquina Bay, Oregon, by hatchery and wild juvenile salmonids. M.S. Thesis, Oregon State University, Corvallis, 234 p.

PARKER, R. R.
1968. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. J. Fish. Res. Board Can. 25:757–794.
1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 28:1503–1510.

PETERMAN, R. M.
1984. Density-dependent growth in early ocean life of sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 41:1825–1829.

PINKAS, L., M. S. OLIPHANT, AND I. L. K. IVERSON.
1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game, Bull. 12, 105 p.

TAYLOR, S. G.
1977. The effect of timing of downstream migration on marine survival of pink salmon (*Oncorhynchus gorbuscha*). M.S. Thesis, Univ. Alaska, Southeastern Senior College, Juneau, 40 p.

THEDINGA, J. F.
1985. Smolt scale characteristics and yield of coho salmon, *Oncorhynchus kisutch*, smolts and adults from Porcupine Creek, southeastern Alaska. M.S. Thesis, Univ. Alaska, Juneau, 93 p.

THORSTEINSON, F. V.
1960. Herring predation on pink salmon fry in a southeastern Alaska estuary. Trans. Am. Fish. Soc. 91:321–323.

WALTERS, C. J., R. HILBORN, R. M. PETERMAN, AND M. J. STALEY.
1978. Model for examining early ocean limitation of Pacific salmon production. J. Fish. Res. Board Can. 35:1303–1315.

GROWTH THROUGH THE FIRST SIX MONTHS OF ATLANTIC COD, *GADUS MORHUA*, AND HADDOCK, *MELANOGRAMMUS AEGLEFINUS*, BASED ON DAILY OTOLITH INCREMENTS[1]

GEORGE R. BOLZ AND R. GREGORY LOUGH[2]

ABSTRACT

Daily growth increments of otoliths from larval and juvenile Atlantic cod and haddock were enumerated, and growth curves were derived describing the first six months of life. Growth for both species was best described by Gompertz-type curves. Inverse regressive methods were employed to construct general models with confidence limits for predicting age (days) for given standard lengths (mm) from hatching through the juvenile period. Microstructural analysis of the otoliths did not discern a settling check at the time when the fish would be expected to leave the pelagic lifestyle for the demersal one, which indicates that the transition is neither physiologically stressful nor abrupt.

Fluctuations in the year-class strength of fish stocks are thought to be determined by the rate of mortality during the first year of life (Moser 1981; Lough et al. 1985; Neilson and Geen 1986; and others). Calculation of reliable mortality rates, assessment of the influences of size-selectivity, and establishment of precise hatching dates and times during a given year when loss to recruitment is greatest are dependent upon accurate age and abundance estimates. Recently, investigators have suggested that mortality during the postlarval and juvenile periods may be as critical as that occurring in the egg and larval life stages (Cohen and Grosslein 1982; Sissenwine 1984). Investigation of this hypothesis by the Northeast Fisheries Center (NEFC) has been ongoing since 1984. Enumeration of daily growth increments deposited on fish otoliths provides the best method for the age determination of larvae and juveniles needed for generating growth curves and estimating mortality (Essig and Cole 1986). An excellent review of past and current methodologies employed in the study and application of otolith microstructure may be found in Campana and Neilson (1985).

Atlantic cod and haddock are both spring spawners on Georges Bank (Sherman et al. 1984) and have pelagic eggs and larvae that undergo similar development. Transformation to the juvenile life stage occurs around 20–30 mm SL, or 2–3 months from hatching (Fahay 1983). The transition from the pelagic to demersal habitat of the adults takes place sometime after transformation, usually by 6–8 cm in midsummer, and recent field observations by the NEFC indicates the transition is a gradual process with considerable variability.

In an earlier study by Bolz and Lough (1983), growth curves were developed for larval Atlantic cod and haddock based on otolith analysis that defined growth from hatching (4–5 mm SL) through the first two months of life (ca. 20 mm SL). Juvenile Georges Bank Atlantic cod and haddock are not fully vulnerable to bottom-trawl gear (Clark et al. 1982), and growth curves based on groundfish surveys conducted by the NEFC in the autumn and spring are inaccurate for fish younger than about six months of age. The primary goal of the work reported here was to derive age-at-length curves for field-caught Atlantic cod and haddock describing their growth from hatch until they are fully available to capture by bottom-trawl survey gear. A secondary objective was to determine if a check ring, a wide incremental band indicative of physiological or environmental changes, was deposited during the juvenile's transition from the pelagic to the demersal mode of life.

METHODS

Atlantic cod and haddock larvae and juveniles were collected on six cruises conducted by the NEFC's RV *Albatross IV* and RV *Delaware II* on

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Georges Bank during the springs of 1981, 1983, and 1984 and the summers of 1984 and 1985. Sample dates and station locations where larvae and juveniles were collected for otolith analysis are given in Table 1. The samples were collected with either 1) a continuous double-oblique haul using a 61 cm bongo net sampler (0.505 and 0.333 mm mesh) deployed to a maximum depth of 100 m (Posgay and Marak 1980), 2) a 1 m MOCNESS[3] fitted with nine 0.333 mm mesh nets which sampled discrete vertical strata from the bottom of the water column to the surface, 3) a 10 m MOCNESS (3 mm mesh) with five nets fished in the same manner as the 1 m MOCNESS (Wiebe et al. 1976, 1985), or 4) a Yankee 36 otter trawl towed for 30 minutes (Grosslein 1974). Stations with high densities of Atlantic cod and haddock larvae and juveniles in good condition were selected during the cruises for otolith analysis. The fish were removed immediately following the haul and preserved in 95% ethanol.

In the laboratory, larvae and juveniles representative of the entire size-range collected were selected for analysis. The standard length, as well as several other morphometric measurements of each larva or juvenile, was measured to the nearest 0.1 mm prior to removal of their otoliths. The 2 sagittae, 2 lapilli, and, when possible, 2 asterisci were dissected from the fish and, excepting juvenile sagittae, mounted whole on microscope slides with Permount[4]. The growth increments (Fig. 1A) on most of these otoliths were

[3]Multiple Opening/Closing Net and Environmental Sensing System.

[4]References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Station information for Atlantic cod and haddock specimens collected for otolith analysis by 61 cm bongo net (0.505 mm mesh) oblique hauls (6B5), 1 m MOCNESS (0.333 mm mesh) discrete vertical hauls (1M3), 10 m MOCNESS (3.0 mm mesh) discrete vertical hauls (10M), and Yankee 36 otter trawl (Y36) during the 1981, 1983, and 1984 survey seasons.

Station	Lat. N	Long. W	Date	Time GMT (Night or day)	Gear	Bottom depth (m)	Number of fish	
							Cod	Haddock
1981	*Albatross IV*	81–03						
54	41°10′	67°06′	24 April	1235(D)	6B5	62	19	—
55	41°13′	67°02′	24 April	1330(D)	6B5	62	10	—
56	41°18′	66°58′	24 April	1450(D)	6B5	66	16	—
57	41°22′	66°55′	24 April	1630(D)	6B5	66	13	—
58	41°26′	66°51′	24 April	1840(D)	6B5	71	12	—
160	41°22′	67°00′	26 April	0645(N)	1M3	63	32	—
1981	*Albatross IV*	81–05						
190	40°57′	67°19′	22 May	0300(N)	1M3	76	—	8
197	40°55′	67°13′	25 May	1200(D)	1M3	80	—	16
205	40°55′	67°09′	26 May	1130(D)	1M3	80	—	6
211	41°11′	67°35′	27 May	1200(D)	1M3	49	—	27
215	41°12′	67°36′	27 May	2330(D)	1M3	40	—	19
1983	*Albatross IV*	83–03						
415	40°54′	67°32′	13 May	1816(D)	1M3	74	7	2
418	40°56′	67°35′	14 May	0456(D)	1M3	71	11	16
421	40°51′	67°34′	14 May	1026(D)	1M3	68	2	13
432	40°47′	67°26′	15 May	1636(D)	1M3	89	1	—
434	40°46′	67°24′	15 May	2229(D)	1M3	93	2	—
438	41°05′	67°47′	16 May	1147(N)	1M3	54	—	15
440	41°09′	67°54′	16 May	1646(N)	1M3	52	3	3
442	41°08′	67°48′	16 May	2222(N)	1M3	40	10	—
444	41°09′	67°55′	17 May	0504(N)	1M3	52	13	—
1984	*Albatross IV*	84–05						
519	41°19′	67°19′	18 June	0319(N)	10M	47	—	30
1984	*Delaware II*	84–07						
76	40°53′	66°22′	15 Aug.	1744(D)	Y36	66	1	1
85	41°50	66°26′	16 Aug.	1045(D)	Y36	78	—	1
88	41°49′	66°23′	16 Aug.	1430(D)	Y36	62	—	1
89	41°47°	66°18′	16 Aug.	1604(D)	Y36	68	—	4
90	41°47′	66°24′	16 Aug.	1715(D)	Y36	78	—	3
91	41°47′	66°30′	16 Aug.	1821(D)	Y36	72	—	1
93	41°45′	66°30′	16 Aug.	2024(D)	Y36	75	—	1
94	41°42′	66°25′	16 Aug.	2124(D)	Y36	75	—	1
98	41°47′	66°11′	17 Aug.	0249(N)	Y36	70	4	—
1984	*Albatross IV*	84–09						
18	41°49′	66°16′	12 Sept.	0845(N)	Y36	70	—	9
19	41°52′	66°21′	12 Sept.	0951(N)	Y36	90	1	12

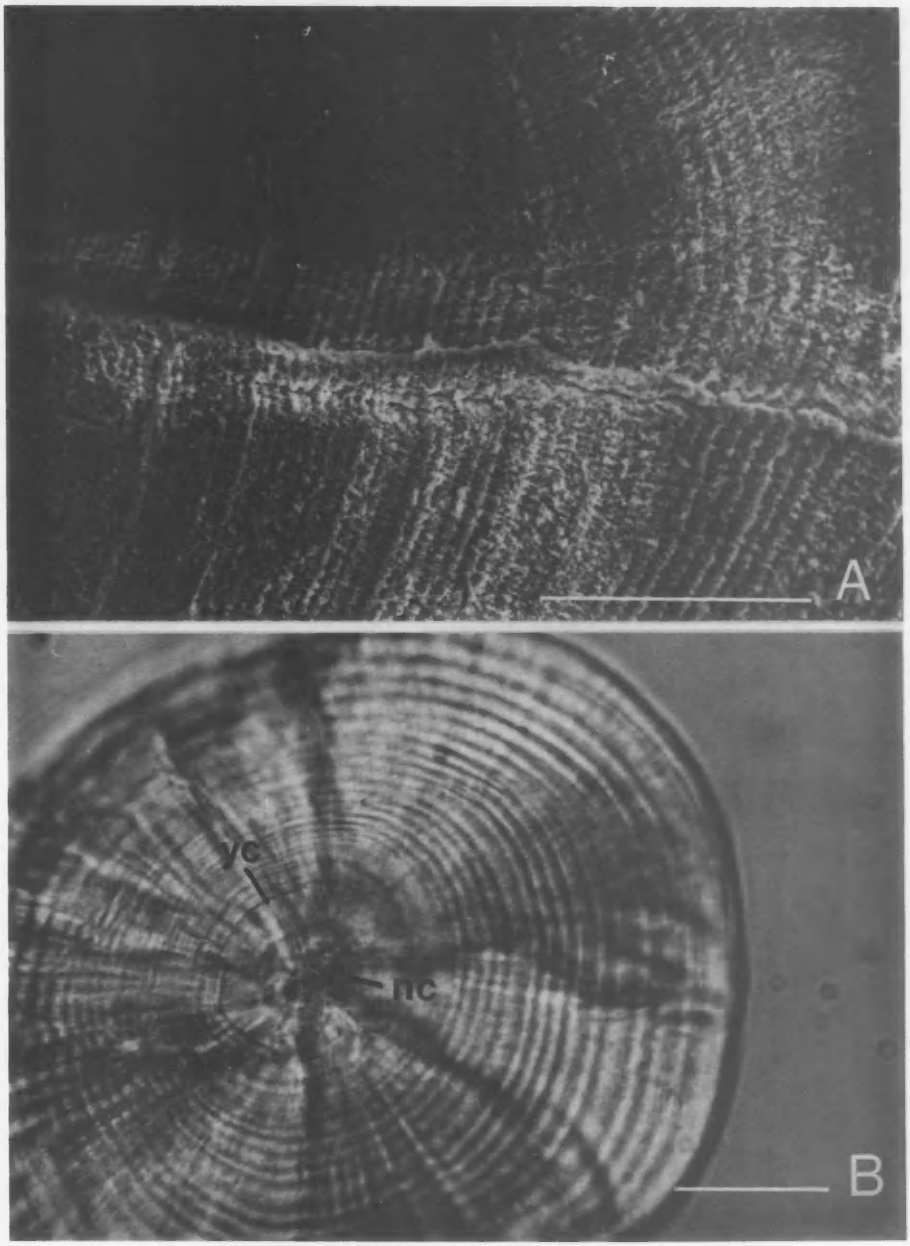


FIGURE 1.—A. Scanning electron micrograph for a portion of the sagitta from a 5-yr-old Atlantic cod, 79 cm SL, showing daily growth increments. Bar of photograph represents 100 μm. B. Sagitta from 47-d-old Atlantic cod larva, 13.3 mm SL (630×). Bar of photograph represents 20 μm. nc = nuclear check, yc = yolk-sac check.

discernible without any further preparation. Sagittae from fish >25 mm SL were mounted in epoxy resin and were ground, above and below, with carborundum paper (600 grit). The resulting thin section was secured to a microscope slide with epoxy resin and etched with 6% EDTA (pH 7.0). Both the grinding and etching procedures were monitored periodically by viewing the sagitta under a dissecting microscope.

The sagittae were then viewed under a Zeiss compound microscope with transmitted light. The number of growth increments were counted from the image projected by a drawing tube onto a Zeiss MOP Digital Image Analyzer System. Under transmitted light each growth increment was composed of a light and dark ring (Fig. 1B), which corresponded to the heavily calcified incremental zone and the organic-rich discontinuous zone of Watabe et al. (1982). Depending on the size of the otolith, magnifications used ranged from 400× to 1,000×. Three counts were made on one of the 2 sagittae from each larva or juvenile, and those otoliths with a repeatable increment count of >90% were used in the growth analysis. The other sagitta was counted once for comparison, as were the 2 lapilli. The number of increments on the 2 asterisci also were enumerated. It was found in the previous study (Bolz and Lough 1983) that the asterisci were not detectable at hatching, in contrast to the sagittae and lapilli, but appeared later in the larval period. This was reflected in the asterisci having on average 27 fewer growth increments than the sagittae. In those instances where the sagittae and lapilli were particularly difficult to read, the number of asteriscal increments plus 27 was consulted as an additional check. Maximum and minimum diameters and planar surface area of the entire otolith were measured routinely on all sagittae, lapilli, and asterisci.

The differential shrinkage of Atlantic cod and haddock larvae and juveniles with respect to standard length was corrected using Theilacker's algorithm (1980), which is specified and discussed in Bolz and Lough (1983). All lengths referred to in the results and discussion portions of this paper are reported as corrected lengths.

RESULTS

Haddock Larval and Juvenile Growth

From analysis of the 189 larval and juvenile haddock, ranging from 3.5 to 123.4 mm SL, we found that growth was best described by a Gompertz-type curve. Previous uses of the Gompertz growth curve and methodology for fitting the curve are described in Pennington (1979), Lough et al. (1982), and Messieh et al. (1987). The variance was stabilized by using the natural log form of the growth equation, and parameters were derived by nonlinear estimation techniques resulting in the relationship:

$$\ln(L) = 1.1987 + 4.8438(1 - e^{-0.0088R}), \quad (1)$$

where L = standard length in mm, and
R = number of days (increments) from hatch.

A plot of the Gompertz curve fitted to the natural log of standard length vs. age in days is shown in Figure 2.

The predicted hatch-length from the curve of 3.32 mm falls within the range of previous studies (Colton and Marak 1969; Fahay 1983). An average growth rate of 0.24 mm/day (Table 2) for the first 30 days is also reasonable (Laurence 1978; Laurence et al. 1981) and agrees with the earlier study of Bolz and Lough (1983). As a generalized model the Gompertz equation described haddock growth through the first six months (175 days), at which point it intersected (Fig. 3) the von Bertalanffy growth curve generated from an analysis of adult haddock by Clark et al. (1982):

TABLE 2.—Mean standard length at age, 95% confidence limits, and growth rate (mm/day and %/day) of larval and juvenile haddock from hatch through 200 days estimated from the Gompertz growth model fit.

Age (d)	Mean length (mm)	95% confidence limits		Growth rate (mm/day)	Growth rate (%/day)
		Lower	Upper		
0	3.32	3.22	3.41	0.14	4.22
10	4.99	4.88	5.11	0.20	4.01
20	7.27	7.13	7.41	0.26	3.58
30	10.25	10.07	10.42	0.34	3.32
40	14.03	13.80	14.26	0.42	2.99
50	18.70	18.39	19.02	0.51	2.78
60	24.34	23.89	24.80	0.61	2.55
70	30.98	30.34	31.63	0.71	2.32
80	38.63	37.74	39.53	0.82	2.12
90	47.27	46.08	48.51	0.91	1.95
100	56.88	55.30	58.50	1.01	1.77
110	67.37	65.35	69.45	1.09	1.63
120	78.67	76.14	81.28	1.17	1.49
130	90.66	87.56	93.86	1.23	1.35
140	103.23	99.52	107.08	1.28	1.23
150	116.26	111.88	120.81	1.32	1.14
160	129.63	124.54	134.92	1.35	1.04
170	143.21	137.38	149.28	1.36	0.95
180	156.88	150.29	163.76	1.37	0.87
190	170.54	163.17	178.25	1.36	0.80
200	184.09	175.92	192.63	1.35	0.73

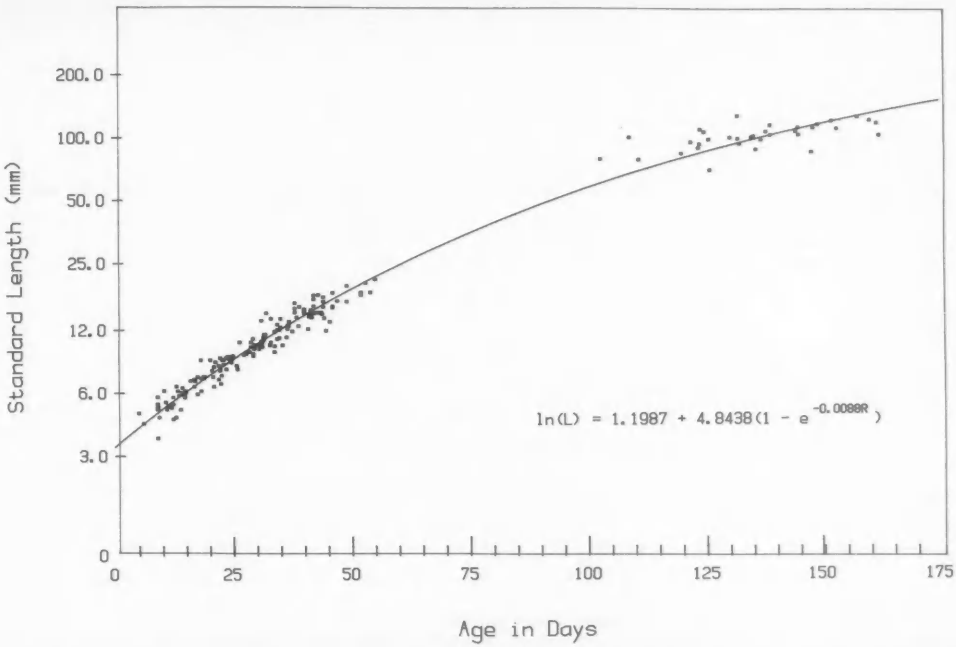


FIGURE 2.—Gompertz growth curve and equation fitted to plot of ln standard length and number of otolith increments (estimated age in days) for 189 larval and juvenile haddock collected on Georges Bank.

$$L = 738.0(1 - e^{-0.3763[(R+D)/365-0.1649]}), \quad (2)$$

where D = Julian date of hatch.

Based on the 1981 season, an average hatch-date of 15 April (D = 105) was employed in the present model. An average length of 19.9 cm would have been attained on 1 January, by fisheries science convention the date at which an individual is considered to be 1-year-old.

Atlantic Cod Larval and Juvenile Growth

Although there were few larger individuals amongst the 157 larval and juvenile Atlantic cod examined, the apparent pattern was similar to that seen in haddock. A Gompertz growth curve also provided a good fit when the natural log of standard length (range: 4.6–104 mm) was plotted (Fig. 4) against age in days (range: 7–151):

$$\ln(L) = 1.3915 + 6.2707(1 - e^{-0.0053R}). \quad (3)$$

The predicted hatch-length of 4.02 mm was within known limits (Colton and Marak 1969). The average growth rate of 0.21 mm/day (Table 3) through the first month was slightly lower than that of haddock, which is consistent with previous findings (Bolz and Lough 1983). At approximately 192 days the larval and juvenile growth curve intersected the von Bertalanffy curve calculated for adult Atlantic cod by Penttila and Gifford (1976):

$$L = 1481.0(1 - e^{-0.1200((R+D)/365-0.6160)}). \quad (4)$$

For purposes of the model a mean hatch-date of 15 March (D = 74) was assumed. An average Atlantic cod would be expected to have achieved a length of 26.1 cm by 1 January (Fig. 5).

Predictability

Since it is desirable, especially during field surveys when direct analysis of otoliths is impossible, to be able to predict age from a given length,

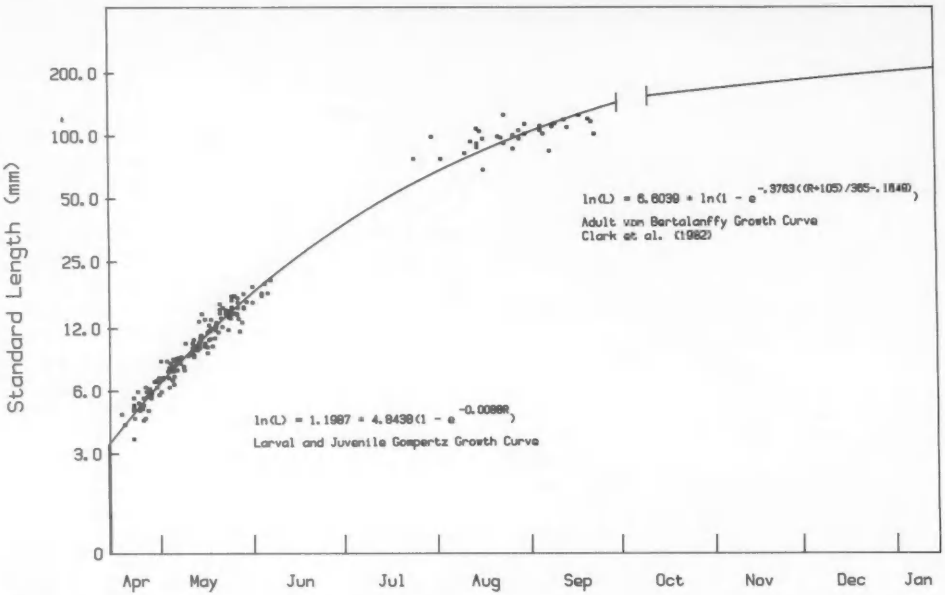


FIGURE 3.—Haddock growth model with an assumed mean hatch-date of 15 April projected through mid-January. An average length of 19.9 cm would have been attained on 01 January, by fisheries science convention the date at which an individual is considered to be 1-year-old.

inverse regression (Draper and Smith 1966) was performed on the Atlantic cod and haddock growth curves to establish confidence intervals for predicting age from a given standard length. In its reduced form the equation obtained for haddock was

$$\frac{X_u}{X_l} = \frac{\ln(1 - (X_0 \pm 0.023t(((X_0 - 0.2990)^2/7.7959) + (1 + 1/n))^{1/2}))}{-0.0088} \quad (5)$$

where X_u and X_l = upper and lower confidence limits,
$X_0 = 1 - e^{-0.0088R}$, and
n = sample size.

Figure 6 shows the fitted growth curve bracketed by 95% confidence intervals.

Performing the same calculations on the Atlantic cod growth curve yielded the relationship:

$$\frac{X_u}{X_l} = \frac{\ln(1 - (X_0 \pm 0.022t(((X_0 - 0.1918)^2/0.9294) + (1 + 1/n))^{1/2}))}{-0.0053} \quad (6)$$

where $X_0 = 1 - e^{-0.0053R}$.

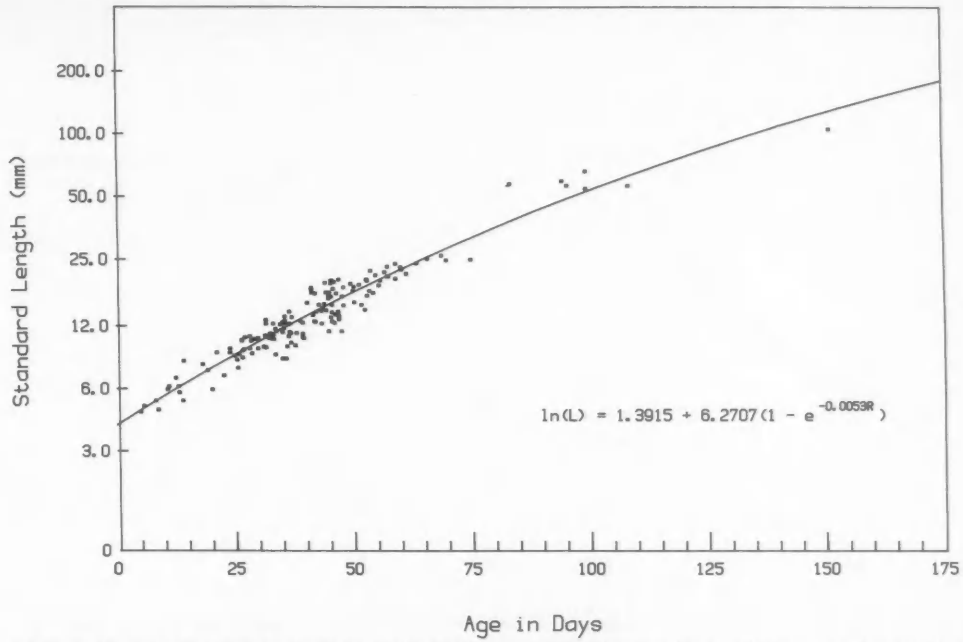


FIGURE 4.—Gompertz growth curve and equation fitted to plot of ln standard length and number of otolith increments (estimated age in days) for 157 larval and juvenile Atlantic cod collected on Georges Bank.

TABLE 3.—Mean standard length at age, 95% confidence limits, and growth rate (mm/day and %/day) of larval and juvenile Atlantic cod from hatch through 200 days estimated from the Gompertz growth model fit.

Age (d)	Mean length (mm)	95% confidence limits		Growth rate (mm/day)	Growth rate (%/day)
		Lower	Upper		
0	4.02	3.79	4.27	0.13	3.37
10	5.56	5.31	5.82	0.18	3.24
20	7.55	7.30	7.82	0.23	3.05
30	10.11	9.85	10.37	0.29	2.87
40	13.32	13.03	13.62	0.36	2.70
50	17.31	16.88	17.75	0.44	2.60
60	22.19	21.48	22.92	0.54	2.43
70	28.08	26.95	29.26	0.64	2.31
80	35.11	33.40	36.91	0.76	2.19
90	43.39	40.91	46.03	0.90	2.10
100	53.05	49.58	56.77	1.04	1.98
110	64.18	59.48	69.26	1.19	1.87
120	76.90	70.69	83.65	1.35	1.77
130	91.27	83.26	100.05	1.52	1.68
140	107.38	97.24	118.57	1.70	1.58
150	125.27	112.65	139.30	1.88	1.51
160	144.99	129.52	162.30	2.06	1.43
170	166.55	147.85	187.61	2.25	1.35
180	189.95	167.61	215.26	2.43	1.28
190	215.17	188.79	245.24	2.61	1.22
200	242.18	211.34	277.52	2.79	1.16

Figure 7 shows the Atlantic cod growth curve bracketed by 95% confidence intervals. Tables 4 and 5 provide predicted ages of Atlantic cod and haddock for given standard lengths with 70% and 95% confidence limits.

Otolith Growth

In the earlier study of larval Atlantic cod and haddock (Bolz and Lough 1983), it was found that the sagittal rings (one incremental and one discontinuous zone) were segregated into distinct regions separated by thicker, darker discontinuous zones referred to as checks or check rings. Two "heavy rings" were noted in the larvae: 1) a nuclear check surrounding a central, amorphous core and 1 or 2 irregular rings, and 2) a yolk-sac check 2–8 increments farther outward (Fig. 1B). The present study corroborated the existence of these two checks. Although each otolith was carefully examined for the presence of a settling check, no regularly occurring heavy ring could be discerned beyond the yolk-sac check in either the haddock or the Atlantic cod juveniles. It should,

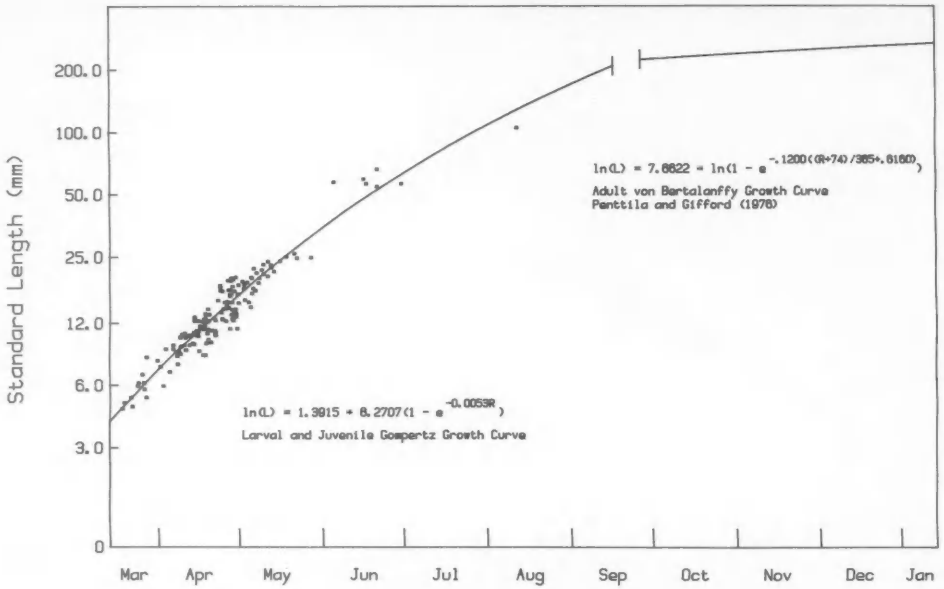
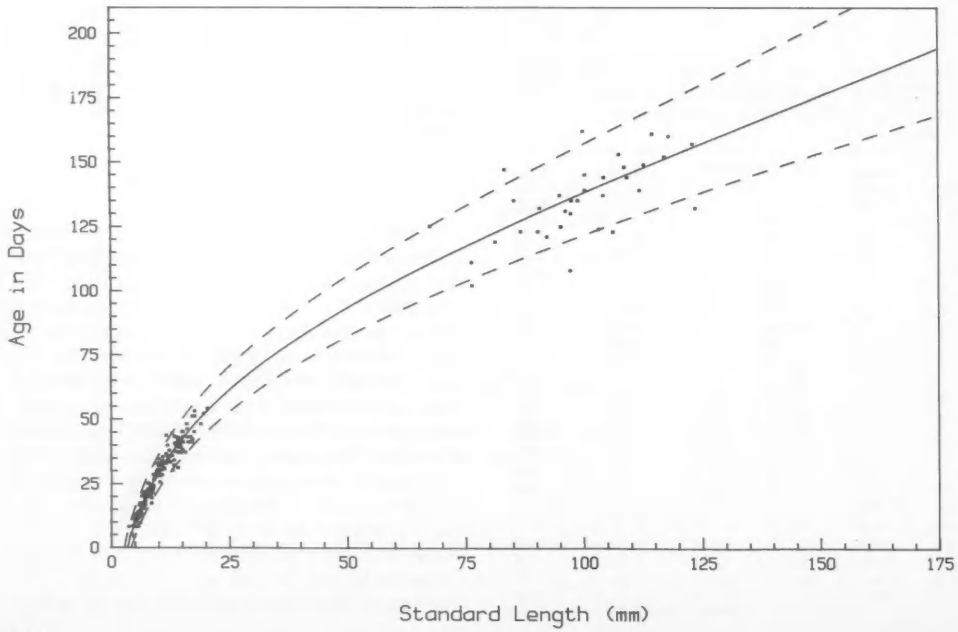


FIGURE 5.—Atlantic cod growth model with assumed mean hatch-date of 15 March projected through mid-January. An average length of 26.1 cm would have been attained by 01 January, by fisheries science convention the date at which an individual is considered to be 1-year-old.



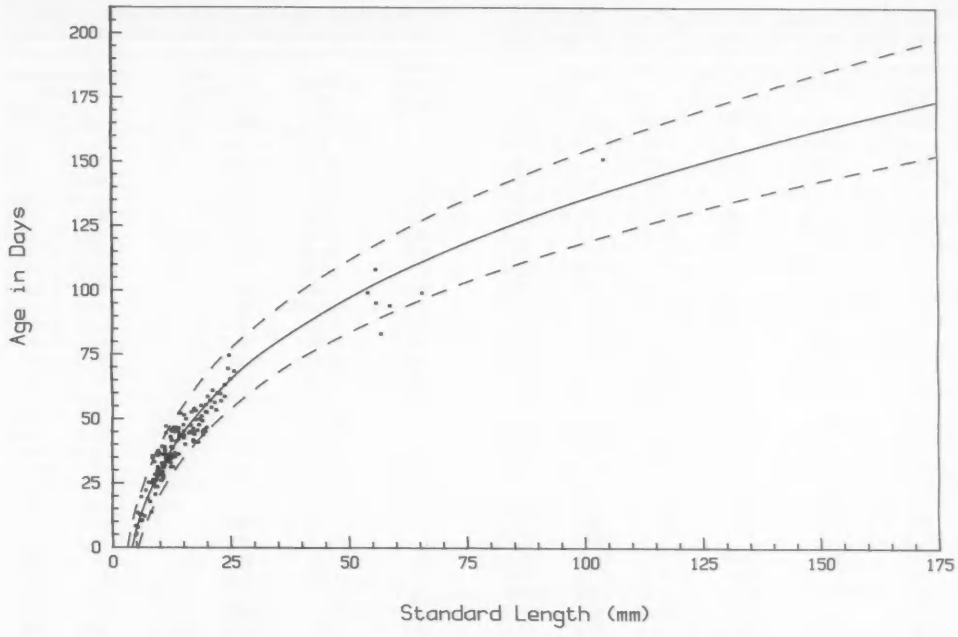


FIGURE 7.—Inverse regression of Atlantic cod growth curve with 95% confidence intervals for predicting age in days for a given standard length (mm).

however, be noted that the size range available for study limited the search for a settling check to individuals >90 mm SL and does not preclude the possibility that thinner, less discernible checks may be found when greater numbers of juveniles 50–90 mm SL are analyzed.

In both haddock and Atlantic cod diametral growth (μm) of the sagittae, lapilli, and asterisci was linearly related to standard length (mm) throughout the larval and juvenile periods. The high correlation ($r > 0.98$) of this relationship and its good agreement with measurements made by Bergstad (1984) would allow the sagittal diameter to be used as a check on the predictability model outlined in Equations (5) and (6) for estimating age from standard length. Estimated ages for haddock larvae and juveniles based on maximum otolith diameters may be obtained with the following equation:

$$Y = 28.390 + 2.413X_1 + 21.561X_2 + 73.841X_3 \quad (7)$$

where Y = estimated age in days,
X_1 = sagittal diameter in mm,
X_2 = lapillus diameter in mm, and
X_3 = astericus diameter in mm.

Table 6 provides a comparison of estimated ages derived from otolith diameters with observed ages derived from the number of daily increments. Although multiple regression analysis using the three otolith diameters yielded a high correlation coefficient ($r = 0.9890$) and nonsignificant t-values, the 95% confidence limits are quite broad (±2 weeks) and should be used with caution. Use of the sagittal diameter alone ($Y = 35.945 + 18.484X_1$) provided a good fit ($r = 0.9861$) for juveniles >90 mm SL but was a poor age predictor for younger fish. If only the sagitta is available for analysis, the relationship:

FIGURE 6.—Inverse regression of haddock growth curve with 95% confidence intervals for predicting age in days for a given standard length (mm).

TABLE 4.—Predicted age in days with 70% and 95% confidence limits of larval and juvenile haddock for a given standard length.

Observed standard length (mm)	Predicted age (d)	70% confidence limits		95% confidence limits	
		Lower	Upper	Lower	Upper
5	10.0	7.1	13.0	4.4	15.9
10	29.3	25.8	32.8	22.7	36.2
15	42.3	38.4	46.3	34.9	50.1
20	52.5	48.2	56.9	44.4	61.1
25	61.1	56.5	65.8	52.4	70.4
30	68.6	63.8	73.7	59.4	78.7
35	75.4	70.3	80.8	65.7	86.1
40	81.7	76.2	87.4	71.4	93.0
45	87.5	81.7	93.5	76.7	99.5
50	92.9	86.9	99.3	81.6	105.6
55	98.1	91.8	104.8	86.3	111.4
60	103.1	96.5	110.0	90.7	117.0
65	107.8	101.0	115.1	95.0	122.4
70	112.4	105.3	120.0	99.0	127.6
75	116.8	109.4	124.8	103.0	132.7
80	121.1	113.5	129.4	106.8	137.7
85	125.3	117.4	133.9	110.4	142.6
90	129.5	121.2	138.4	114.0	147.4
95	133.5	124.9	142.8	117.5	152.2
100	137.5	128.6	147.1	121.0	156.9
105	141.4	132.2	151.4	124.3	161.6
110	145.2	135.8	155.6	127.6	166.2
115	149.0	139.3	159.8	130.9	170.8
120	152.8	142.7	163.9	134.1	175.4
125	156.6	146.1	168.1	137.2	180.0
130	160.3	149.5	172.2	140.4	184.6
135	164.0	152.9	176.3	143.4	189.2
140	167.6	156.2	180.4	146.5	193.9
145	171.3	159.5	184.6	149.5	198.5
150	175.0	162.8	188.7	152.5	203.2
155	178.6	166.0	192.8	155.5	207.9
160	182.3	169.3	197.0	158.5	212.7
165	185.9	172.6	201.2	161.4	217.5
170	189.6	175.8	205.4	164.3	222.4
175	193.3	179.0	209.6	167.3	227.4

TABLE 5.—Predicted age in days with 70% and 95% confidence limits of larval and juvenile Atlantic cod for a given standard length.

Observed standard length (mm)	Predicted age (d)	70% confidence limits		95% confidence limits	
		Lower	Upper	Lower	Upper
5	6.7	2.1	11.3	−2.1	15.7
10	29.6	24.5	34.8	19.9	39.8
15	44.5	39.0	50.1	34.0	55.5
20	55.8	49.9	61.8	44.7	67.6
25	65.0	58.9	71.3	53.4	77.5
30	72.9	66.5	79.6	60.8	86.0
35	79.9	73.2	86.8	67.3	93.5
40	86.1	79.2	93.3	73.1	100.3
45	91.8	84.7	99.2	78.3	106.5
50	97.0	89.7	104.7	83.2	112.2
55	101.9	94.3	109.8	87.6	117.6
60	106.4	98.7	114.6	91.8	122.6
65	110.7	102.7	119.1	95.7	127.3
70	114.7	106.6	123.3	99.4	131.8
75	118.6	110.3	127.4	102.9	136.1
80	122.3	113.8	131.3	106.3	140.2
85	125.8	117.1	135.0	109.5	144.1
90	129.2	120.3	138.6	112.5	147.9
95	132.4	123.4	142.0	115.5	151.6
100	135.6	126.4	145.4	118.3	155.1
105	138.6	129.2	148.6	121.0	158.6
110	141.5	132.0	151.7	123.7	161.9
115	144.4	134.7	154.8	126.3	165.1
120	147.2	137.3	157.7	128.7	168.3
125	149.9	139.9	160.6	131.1	171.3
130	152.5	142.3	163.4	133.5	174.3
135	155.1	144.8	166.1	135.8	177.3
140	157.6	147.1	168.8	138.0	180.2
145	160.0	149.4	171.4	140.2	183.0
150	162.4	151.6	174.0	142.3	185.7
155	164.8	153.8	176.5	144.4	188.5
160	167.1	156.0	179.0	146.4	191.1
165	169.3	158.1	181.4	148.4	193.7
170	171.5	160.2	183.8	150.4	196.3
175	173.7	162.2	186.2	152.3	198.8

$$Y = 11.875 + 112.654X_1,\ r = 0.9129 \qquad (8)$$

should be used for the larval and postlarval period.

The equation for the estimated ages of larval and juvenile Atlantic cod (Table 7) is as follows:

$$Y = 48.202 + 8.628X_1 - 121.908X_2 + 139.733X_3,$$

$$r = 0.9292. \qquad (9)$$

When using only the sagittal diameter, the following relationship should be applied to larvae and postlarvae:

$$Y = 19.364 + 89.560X_1,\ r = 0.8659. \qquad (10)$$

Unlike the tedious laboratory methods needed for the enumeration of otolith increments, gross measurements on a limited number of juvenile otoliths could be performed at sea.

DISCUSSION

Despite the tedious methodology required for enumerating daily growth increments in larval and juvenile otoliths, the present work suggests that it is feasible to construct age-length keys for Atlantic cod and haddock similar to those commonly applied in adult population studies (Clark et al. 1982). The value of such growth data is based on several assumptions, however. Since all conclusions drawn depend upon it, reasonable assurance of the day-increment relationship in the species being investigated is critical (Beamish and McFarlane 1987; Geffen 1987). Confidence in the growth models generated here for Atlantic cod and haddock may be found in the following inferences: 1) the predicted hatch lengths of 3.32 mm for haddock and 4.02 mm for Atlantic cod fall within known limits; 2) a high correlation for the length-at-age data with the rearing experiments of Laurence et al. (1981); and 3) the smooth-

TABLE 6.—Estimated age in days based on otolith diameters with 95% confidence limits for larval and juvenile haddock compared with observed age derived from number of daily increments.

Observed age (d)	Estimated age (d)	95% confidence limits	
		Lower	Upper
0.0	1.5	−12.3	15.4
10.0	11.3	−2.5	25.1
20.0	21.1	7.4	34.9
30.0	30.9	17.2	44.6
40.0	40.7	27.0	54.4
50.0	50.5	36.8	64.2
60.0	60.3	46.7	73.9
70.0	70.1	56.5	83.7
80.0	79.9	66.2	93.6
90.0	89.7	76.0	103.3
100.0	99.5	85.8	113.1
110.0	109.3	95.6	122.9
120.0	119.0	105.3	132.8
130.0	128.8	115.1	142.6
140.0	138.6	124.8	152.5
150.0	148.4	134.5	162.3
160.0	158.2	144.3	172.2
170.0	168.0	154.0	182.0
180.0	177.8	163.7	191.9

TABLE 7.—Estimated age in days based on otolith diameters with 95% confidence limits for larval and juvenile Atlantic cod compared with observed age derived from number of daily increments.

Observed age (d)	Estimated age (d)	95% confidence limits	
		Lower	Upper
0.0	7.1	−6.9	21.1
10.0	15.8	2.1	29.5
20.0	24.5	11.0	38.0
30.0	33.2	19.9	46.5
40.0	41.9	28.7	55.1
50.0	50.6	37.5	63.8
60.0	59.3	46.2	72.5
70.0	68.0	54.8	81.2
80.0	76.7	63.4	90.1
90.0	85.4	71.9	98.9
100.0	94.1	80.4	107.9
110.0	102.8	88.8	116.9
120.0	111.6	97.2	125.9
130.0	120.3	105.5	135.0
140.0	129.0	113.8	144.1
150.0	137.7	122.1	153.3
160.0	146.4	130.3	162.5
170.0	155.1	138.5	171.7
180.0	163.8	146.6	180.9

ness with which the larval and juvenile curves flow into those independently developed for the adults (Clark et al. 1982; Penttila and Gifford 1976).

The predictive models for Atlantic cod and haddock have to be viewed as general in nature, and the widening of the confidence intervals with increasing length (Tables 4, 5) must be kept in mind. Natural variability of length-at-age and difficulty in the preparation and reading of otoliths increases as the fish becomes older and makes precise age determinations extremely difficult. For example, the ability to predict correctly the age of an individual haddock at the 70% confidence level decreases from ±3 days at 5 mm SL to ±2 weeks at 175 mm. In spite of this problem, otolith aging of field-caught larvae and juveniles provides a degree of precision not possible with indirect methods based on size-frequency analyses (Ebert 1973). Refinement of the estimated means and the reduction and stabilization of the variance should result as a greater number of otoliths are analyzed in the future.

Microstructural examination of larval Atlantic cod and haddock otoliths clearly delineated check rings related to hatching and yolk-sac absorption (Bolz and Lough 1983). Both of these transitions are abrupt, and the dark, thick discontinuous zones readily observable on the otoliths are a reflection of metabolic disturbances undergone at these times. Although additional check rings were noted in 3 or 4 of the juvenile otoliths, there was no regularity with respect to age of their occurrence. In these individuals the checks were probably the result of physiological trauma induced by disease or injury since calcium carbonate secretion ceases not only with the metabolic changes accompanying transitional phases but during times of stress (Morales-Nin 1987). It was suspected that a distinct check, similar to the settling check found by Victor (1982) in the bluehead wrasse, *Thalassoma bifasciatum*, would be found demarcating the transition from the pelagic to the demersal mode of life with its accompanying changes in diet and activity levels. No check rings were found in the transition period (50–100 days) on the otoliths analyzed. This suggests that an abrupt metabolic disturbance does not occur at this phase of the fish's life and that settling near the bottom takes place over an extended period of time (1–2 months) even for individual fish. This agrees with a preliminary finding for Scotian Shelf gadoids by Campana and Neilson (1985). However, in a recent study by Mahon and Neilson (1987) on the gut contents of Scotian Shelf haddock, they concluded that the transition from pelagic to demersal life occurred relatively suddenly, less that a month for the individual fish. Apparently, change to the demersal life stage is not stressful for Atlantic cod and haddock, at least as a metabolic manifestation recorded in their otoliths.

When used in conjunction with length-frequency data collected throughout the year, the Atlantic cod and haddock growth curves presented in this report should allow accurate estimates of the following: 1) peak hatching dates, 2) the number of cohorts produced within a given season, 3) intraseasonal changes in growth and mortality rates of cohorts, and 4) which part of the spawning curve the recruits originated from (Methot 1983). In the future year-to-year comparison of deviations in these estimates could lead to the construction of viable recruitment models permitting the early prediction of year-class strength.

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LITERATURE CITED

BEAMISH, R. J., AND G. A. MCFARLANE.
1987. Current trends in age determination methodology. *In* R. C. Summerfelt and G. E. Hall (editors), Age and growth of fish, p. 15–42. Iowa State Univ. Press, Ames.

BERGSTAD, O. A.
1984. A relationship between the number of growth increments on the otoliths and age of larval and juvenile cod, *Gadus morhua* L. *In* E. Dahl, D. S. Danielssen, E. Mokness, and P. Solemdal (editors), The propagation of cod *Gadus morhua* L, p. 251–272. Flodevigen rapportser. 1, 1984.

BOLZ, G. R., AND R. G. LOUGH.
1983. Growth of larval Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, on Georges Bank, spring 1981. Fish. Bull., U.S. 81:827–836.

CAMPANA, S. E., AND J. D. NEILSON.
1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014–1032.

CLARK, S. H., W. J. OVERHOLTZ, AND R. C. HENNEMUTH.
1982. Review and assessment of the Georges Bank and Gulf of Maine haddock fishery. J. Northwest Atl. Fish. Sci. 3:1–27.

COHEN, E. B., AND M. D. GROSSLEIN.
1982. Food consumption by silver hake (*Merluccius bilinearis*) on Georges Bank with implications for recruitment. *In* G. M. Calliet and C. A. Simenstadt (editors), Gutshop '81, fish food habits studies, p. 286–294. Proc. Third Pac. Workshop, Washington Sea Grant, Univ. Wash. Press, Seattle.

COLTON, J. B., AND R. R. MARAK.
1969. Guide for identifying the common planktonic fish eggs and larvae of continental shelf water, Cape Sable to Block Island. U.S. Bur. Commer. Fish., Biol. Lab., Woods Hole, Mass., Lab. Ref. Doc. 69-9, 43 p.

DRAPER, N. R., AND H. SMITH.
1966. Applied Regression Analysis. Wiley, N.Y.

EBERT, T. A.
1973. Estimating growth and mortality rates from size data. Oecologia 11:281–298.

ESSIG, R. J., AND C. F. COLE.
1986. Methods of estimating larval fish mortality from daily increments in otoliths. Trans. Am. Fish. Soc. 115:34–40.

FAHAY, M. P.
1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. J. Northwest Atl. Fish. Sci. 4:1–423.

GEFFEN, A. J.
1987. Methods of validating daily increment deposition in otoliths of larval fish. *In* R. C. Summerfelt and G. E. Hall (editors), Age and growth of fish, p. 223–240. Iowa State Univ. Press, Ames.

GROSSLEIN, M. D.
1974. Bottom trawl survey methods of the Northeast Fisheries Center, Woods Hole, Massachusetts, U.S. ICNAF Res. Doc. 74/86, Ser. No. 3332.

LAURENCE, G. C.
1978. Comparative growth, respiration and delayed feeding abilities of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as influenced by temperature during laboratory studies. Mar. Biol. (Berl.) 50:1–7.

LAURENCE, G. C., A. S. SMIGIELSKI, T. A. HALAVIK, AND B. R. BURNS.
1981. Implications of direct competition between larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in laboratory growth and survival studies at different food densities. *In* R. Lasker and K. Sherman (editors), The early life history of fish, p. 304–311. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178.

LOUGH, R. G., G. R. BOLZ, M. PENNINGTON, AND M. D. GROSSLEIN.
1985. Larval abundance and mortality of Atlantic herring (*Clupea harengus* L.) spawned in the Georges Bank and Nantucket Shoals areas, 1971–78 seasons, in relation to spawning stock size. J. Northwest Atl. Fish. Sci. 6:21–35.

LOUGH, R. G., M. PENNINGTON, G. R. BOLZ, AND A. A. ROSENBERG.
1982. Age and growth of larval Atlantic herring, *Clupea harengus* L., in the Gulf of Maine-Georges Bank region based on otolith growth increments. Fish. Bull., U.S. 80:187–199.

MAHON, R., AND J. D. NEILSON.
1987. Diet changes in Scotian Shelf haddock during pelagic and demersal phases of the first year of life. Mar. Ecol. Prog. Ser. 37:123–130.

MESSIEH, S. N., D. S. MOORE, AND P. RUBEC.
1987. Estimation of age and growth of larval Atlantic herring as inferred from examination of daily growth increments of otoliths. *In* R. C. Summerfelt and G. E. Hall (editors), Age and growth of fish, p. 433–442. Iowa State Univ. Press, Ames.

METHOT, R. D., JR.
1983. Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. Fish. Bull., U.S. 81:741–750.

MORALES-NIN, B.
1987. Ultrastructure of the organic and inorganic constituents of the otoliths of the sea bass. *In* R. C. Summerfelt and G. E. Hall (editors), Age and growth of fish, p. 331–343. Iowa State Univ. Press, Ames.

MOSER, H. G.
1981. Morphological and functional aspects of marine fish larvae. *In* R. Lasker (editor), Marine fish larvae, p. 90–131. Univ. Wash. Press, Seattle and Lond.

NEILSON, J. D., AND G. H. GEEN.
1986. First-year growth rate of Sixes River chinook salmon as inferred from otoliths: effects on mortality and age at maturity. Trans. Am. Fish. Soc. 115:28–33.

PENNINGTON, M. R.
1979. Fitting a growth curve to field data. *In* J. K. Ord., G. P. Patil, and C. Taillie (editors), Statistical distributions in ecological work, p. 419–428. Int. Coop. Publ. House, Fairland, MD.

PENTTILA, J. A., AND V. M. GIFFORD.
1976. Growth and mortality rates for cod from the Georges Bank and Gulf of Maine areas. Int. Comm. Northwest Atl. Fish. Res. Bull. No. 12, p. 29–36.

POSGAY, J. A., AND R. R. MARAK.
1980. The MARMAP bongo zooplankton sampler. J. Northwest Atl. Fish. Sci. 1:91–99.

SHERMAN, K., W. SMITH, W. MORSE, M. BERMAN, J. GREEN, AND L. EJSYMONT.
1984. Spawning strategies of fishes in relation to circulation, phytoplankton production, and pulses in zooplankton off the northeastern United States. Mar. Ecol. Prog. Ser. 18:1–19.

SISSENWINE, M. P.
1984. Why do fish populations vary? *In* R. May (editor), Exploitation of marine communities, p. 59–94. Springer-Verlag, N.Y.

THEILACKER, G. H.
1980. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. Fish. Bull., U.S. 78:685–692.

VICTOR, B. C.
1982. Daily otolith increments and recruitment in two coral-reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. Mar. Biol. (Berl.) 71:203–208.

WATABE, N., K. TANAKA, J. YAMADA, AND J. M. DEAN.
1982. Scanning electron microscope observations of the organic matrix in the otolith of the teleost fish *Fundulus heteroclitus* (Linnaeus) and *Tilapia nilotica* (Linnaeus). J. Exp. Mar. Biol. Ecol. 58:127–134.

WIEBE, P. H., K. H. BURT, S. H. BOYD, AND A. W. MORTON.
1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. J. Mar. Res. 34:313–326.

WIEBE, P. H., A. W. MORTON, A. M. BRADLEY, R. H. BACKUS, J. E. CRADDOCK, V. BARBER, T. J. COWLES, AND G. R. FLIERL.
1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. Mar. Biol. (Berl.) 87:313–323.

THE RELATION BETWEEN SPAWNING SEASON AND THE RECRUITMENT OF YOUNG-OF-THE-YEAR BLUEFISH, *POMATOMUS SALTATRIX*, TO NEW YORK[1]

ROBERT M. NYMAN[2] AND DAVID O. CONOVER[3]

ABSTRACT

The association between oceanic spawning season and the recruitment of young-of-the-year (YOY) bluefish, *Pomatomus saltatrix*, to the inshore waters of New York was studied by estimating the spawn dates of recruited fish collected in the shore zone from the number of growth increments in their otoliths. Field collections on the south shore of Long Island showed that recruitment of 3–6 cm fork length fish occurred as a distinct pulse during the last week of May in 1985 and the second week of June in 1986. Length-frequency distributions were generally unimodal and most fish collected later could be attributed to this one recruitment episode. The frequency of otolith ring deposition in YOY bluefish was determined by marking the otoliths of field-caged fish with an injection of tetracycline, and then periodically subsampling these over the ensuing 61-day period. Regression analysis indicated a 1:1 relation between the number of days since marking and the number of rings beyond the mark. Back-calculation to the time of first ring deposition revealed that field-collected YOY bluefish from Long Island were spawned primarily in the March–April spawning season reported to occur south of Cape Hatteras. Relatively few fish were collected from the summer spawning season that reportedly occurs in the Middle Atlantic Bight. Almost all of these summer-spawned fish were collected from the Hudson River.

The bluefish, *Pomatomus saltatrix*, supports a major recreational fishery along the Atlantic coast of the United States. In 1985, more bluefish by weight were caught than any other marine fish, accounting for over 24% of the total marine recreational catch (U.S. Department of Commerce 1986). Despite the importance of bluefish to the recreational fishery, very little is known of its early life history.

Bluefish are found over different portions of the continental shelf from Florida to Nova Scotia at various times of the year (Bigelow and Schroeder 1953; Wilk 1977; Gilmore 1985). Based on descriptions of the temporal and spatial abundance of larvae, Kendall and Walford (1979) suggested that there are primarily two distinct spawning periods and regions: a spring spawning in the South Atlantic Bight at the edge of the Florida Current (see also Collins and Stender 1987), and a summer spawning in the Middle Atlantic Bight midway over the continental shelf (see also Morse et al. 1987). They further proposed that the spring-spawned larvae are transported northward in the slope waters and then move inshore, spending their first summer in the bays and estuaries of the Middle Atlantic Bight. Summer-spawned larvae, according to Kendall and Walford, spend their first summer at sea or enter the estuaries of the Middle Atlantic Bight only briefly before migrating southward with the onset of winter. A minor spawning season extending from September to November off the coast of Georgia and Florida (Collins and Stender 1987) involves fish resident to the South Atlantic Bight (Kendall and Walford 1979).

The purpose of this study is to evaluate Kendall and Walford's hypothesis by back-calculating the spawn dates of young-of-the-year (YOY) bluefish that have recruited to inshore waters, from the number of growth increments in their otoliths. First, we describe the timing and pattern of recruitment of YOY bluefish to one segment of the mid-Atlantic coastline: Long Island, NY. If spawning is episodic, and if YOY bluefish from each spawning period enter New York waters, then length-frequency distributions of field collections should be multimodal. Next, we verify that otolith increment deposition has a daily peri-

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odicity in *P. saltatrix*. Finally, the spawning season(s) of YOY bluefish recruiting to New York is determined by ageing and back-calculating to the date of first ring deposition.

METHODS

Seine Collections

The temporal abundance and length-frequency distribution of YOY bluefish was estimated by seining 2–4 times per month from April to October at several sites on Long Island and in the Hudson River (Fig. 1). In 1985 and 1986, three sites in Great South Bay on the south shore of Long Island were sampled: Smith Point County Park, Fireplace Neck, and the Carmans River. Seining was conducted with a 0.6 cm mesh, 30 m net set from shore, either on foot or from a small boat. Water temperature was recorded at each site and date. In 1986, a site on the north shore of Long Island, Setauket Harbor, was also sampled. A few samples were taken in the fall by angling with rod and reel. All specimens were frozen for later measurement of fork length (FL) and weight, and extraction of otoliths.

Additional specimens captured in 1986 from Jamaica Bay and the Hudson River were provided by the New York Department of Environmental Conservation (NYDEC). Their sampling was conducted with a 60 m seine (1.2 cm mesh) set from a boat.

Otolith Preparation and Analysis

The sagittae were mounted concave side down on a glass microscope slide with cyanoacrylate (instant glue). Two layers of masking tape were applied on either side of the otolith. The slide was then turned upside-down and sanded on a strip of wet 1200 grit wet-dry sandpaper. The masking tape ensured that the otolith was sectioned on a consistent plane and helped prevent grinding past the nucleus. Once the nucleus was reached, the otolith was polished on wet felt, using levigated alumina polishing compound. Three replicate counts of each otolith were made under a Zeiss[4] compound microscope with transmitted polarized light at 125–312×. If the three counts differed by more than 10% (which occurred in about 1 out of every 10 otoliths), an additional count was made and the outlier discarded. The three final counts were then averaged. The total length of each otolith was measured (nearest 0.1 mm) with a dissecting microscope using an ocular micrometer.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

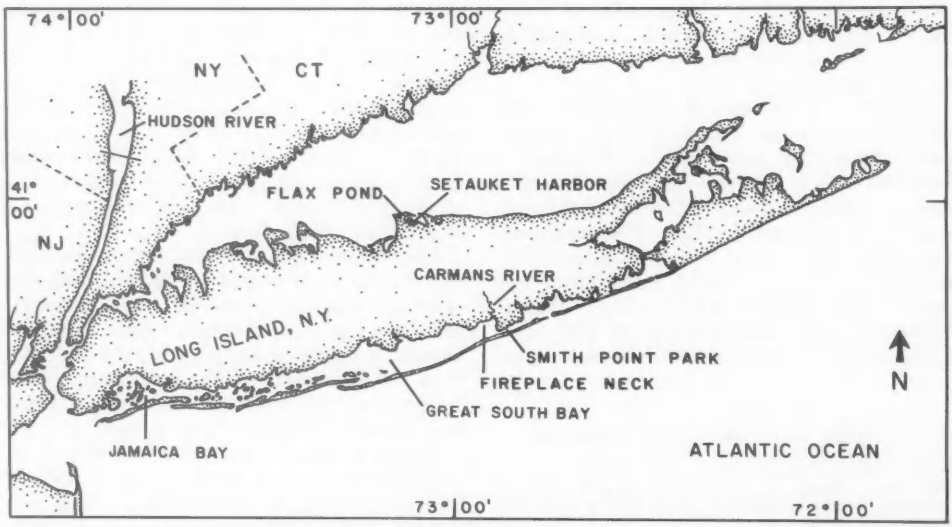

FIGURE 1.—Map of the study area with sampling locations as indicated.

Frequency of Ring Deposition

The frequency of growth ring deposition was determined by marking the otoliths of fish with tetracycline and then subsampling the marked fish at various periods of time thereafter (Campana and Neilson 1982). Sixty YOY bluefish (7–10 cm FL) were captured by seine in Flax Pond, Old Field, NY (Fig. 1) and were transported to the Flax Pond Laboratory of SUNY Stony Brook. The fish were anesthetized in a solution of MS-222 (30 mg/L) and given an intraperitoneal injection of tetracycline (100 mg/kg of fish). After injection, all fish were placed in a 1.3 × 1.3 m cylindrical floating cage constructed out of 5 mm plastic mesh and anchored in Flax Pond. The fish were fed chopped *Menidia menidia* twice a day, and dead bluefish were removed daily. Samples of 5–10 healthy fish were periodically taken from the cage using a dip net and frozen until the otoliths could be excised. The experiment was terminated 61 days after the injections.

After preparation as described above, the tetracycline-treated otoliths were viewed on a Zeiss compound microscope using reflected ultraviolet (UV) light at 160–400×. Tetracycline fluoresces upon exposure to UV light, thus enabling the location of the marked ring to be determined. The UV light was then turned off, and the number of rings from the mark to the edge of the otolith was counted under transmitted white light. Each otolith preparation was coded so that the reader did not know the true age. Three replicate counts were conducted on each otolith.

RESULTS

Temporal Abundance and Length Frequency

Great South Bay

The appearance of YOY bluefish in the shore zone was abrupt in both years of the study. In 1985, no YOY bluefish were caught in weekly samples until 28 May when a catch per unit effort (CPUE = no. fish per seine haul) of 14.0 was recorded (Fig. 2a). Corresponding water temperature was about 20°C. CPUE declined steadily thereafter through October with two exceptions: the large collections on 10 and 28 July were each due to an unusually large number of fish in single seine hauls in the Carmans River. In 1986, YOY bluefish were first caught on 10 June when the water temperature was 24°C. The maximum CPUE (45.3) was obtained on 16 June and was followed by a decrease in CPUE in subsequent collections (Fig. 2b).

Length-frequency distributions in 1985 showed the progression of a single mode through mid-August (Fig. 3a). Newly recruited fish in late May were 3–6 cm FL. Subsequent samples showed an increase in the mean and range of fish lengths, probably due to somatic growth of the initial recruits. There was no evidence of new 3–6 cm recruits entering the shore zone later in the year (Fig. 3a). Although seining continued until November, very few YOY bluefish were caught after August. An additional sample (n = 8) taken on 16 September by angling from a pier on Great South Bay had a mean fork length of 17.8 cm and a range of 14.6–19.5 cm. Length-frequency data from 1986 (Fig. 3b) show a very similar pattern to that in 1985: a single length mode appears in June and these fish increase in size through the summer. Few YOY bluefish were caught in August, September, or October.

Size at recruitment to the shore zone was similar in both years of our study: mean length of the 1985 and 1986 year classes at first appearance in the shore zone was 4.6 and 4.5 cm respectively (Fig. 4). However, because the 1986 year class first appeared in the shore zone two weeks later than did the 1985 year class (Fig. 2), the mean lengths of 1986 year class were less than those of 1985 on comparable dates in June and early July. By mid-July, however, this difference in mean length of the two year classes was no longer apparent. Both year classes reached a size of about 13–14 cm by late August when they rarely appeared in our seine collections.

Setauket Harbor

In 1986, the YOY bluefish did not appear on the north shore of Long Island at Setauket Harbor until 3–6 weeks after they first appeared in Great South Bay. Collections at Setauket Harbor were small at first with only one individual being caught on 1 July and three on 8 July. It was not until 22 July that catches similar in number to those in Great South Bay were being obtained. These fish had similar mean lengths (10.2 cm, n = 87, on 22 July; 11.9 cm, n = 22, on 5 August; 13.9 cm, n = 17, on 20 August) to those on comparable dates from Great South Bay (cf. Fig. 4). Length-frequency distributions by date were unimodal.

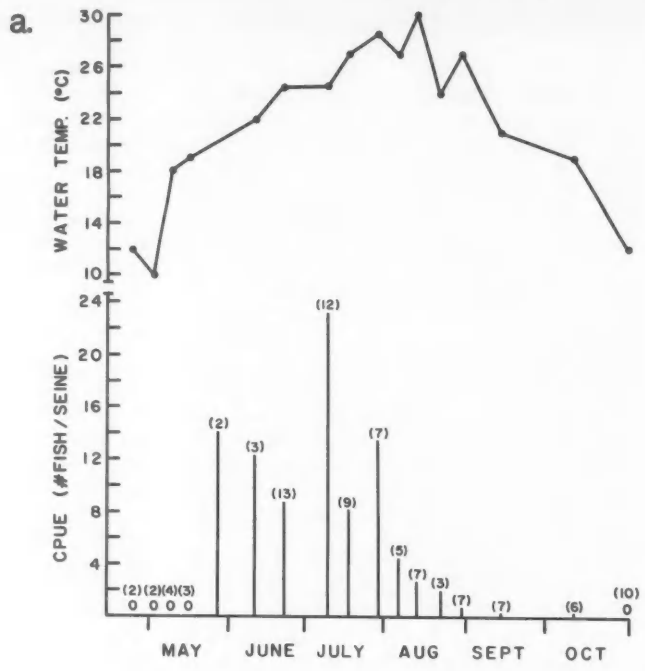

FIGURE 2.—Catch per unit effort (CPUE) of YOY bluefish from Great South Bay, NY, plotted with the mean water temperature

Jamaica Bay and the Hudson River

The length-frequency distributions of YOY bluefish from Jamaica Bay in June, July, and August were similar to those from Great South Bay (Fig. 5). Fish lengths in June were unimodal. Subsequent collections contained progressively larger fish that were also unimodal in length distribution.

Sampling in the Hudson River began on 16 July 1986 and continued through 8 October. The size ranges of YOY bluefish in the July and August samples were similar to those from Great South Bay, although the length distribution on 30 July appears bimodal (Fig. 6). The length distributions from the 10 and 23 September collections were especially broad. In particular, the 23 September sample contained a group of fish that were much smaller (10–14 cm FL) than the mean size at this time in Great South Bay (Fig. 4), together with a second group of larger fish that correspond more closely in size with those collected elsewhere (18–24 cm).

Frequency of Ring Deposition

In tetracycline-injected YOY bluefish, the number of rings beyond the tetracycline mark (Y) and the number of days after injection (X) had a 1:1 correspondence (Fig. 7). The relationship was described by the equation $Y = 0.971X - 0.287$ ($n = 27$, $r = 0.996$). The slope did not differ significantly from 1.0 (t-test, $P > 0.1$).

Growth rate of the caged fish was slightly greater than that of field fish and survival was high (80%) with mortalities occurring only in the first few days of the 61-d experiment. The increase in mean fork length was 1.7 mm/day among the caged fish, as compared with about 1.3 mm/day for fish from field collections during the same time period (Fig. 4). Hence, the caged fish did not appear to be adversely affected by confinement.

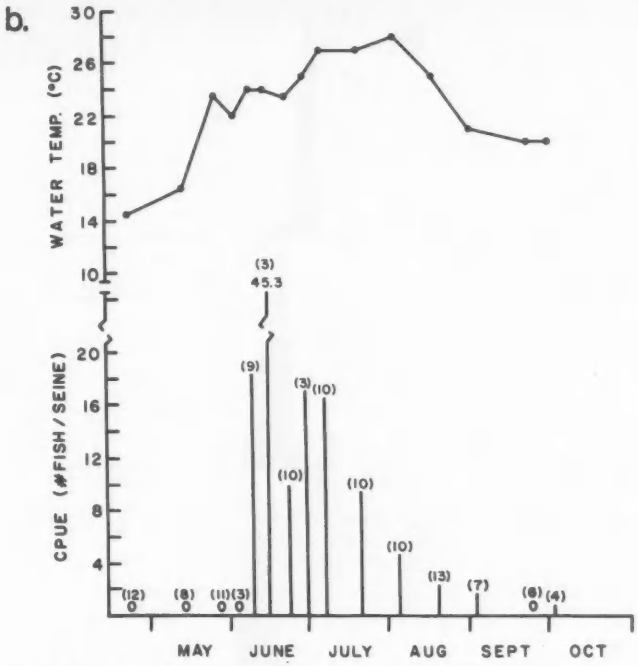

FIGURE 2.—*Continued*—on each sampling date. (a) 1985; (b) 1986. Number of seine hauls is in ().

Back-Calculated Date of First Ring Deposition

A representative sample of 169 YOY bluefish ($n = 88$ from 1985, $n = 81$ from 1986) captured in Great South Bay were aged by counting the total number of otolith rings. The date of first ring deposition for each aged fish was then calculated based on the date of capture. In both 1985 and 1986, the dates of first ring deposition for YOY bluefish were predominantly in March and April (Fig. 8a, b).

Four fish from each of the two apparent length modes in the 30 July collection from the Hudson River (Fig. 6) were aged to determine if these represented a difference in spawning season. The fish examined were 7.8–13.8 cm in size, and back-calculated dates of first ring deposition extended from 7 to 30 April. Hence, these fish could all be attributed to the same spring spawning period as those from the south shore of Long Island.

However, YOY bluefish from the smaller (10–14 cm) size class caught on 23 September in the Hudson River (Fig. 6) were also aged and their back-calculated dates of first ring deposition were found to be predominantly in June and July, and to a lesser extent in May (Fig. 8c). These dates differed greatly from those of fish captured earlier in the year in the Hudson River, and along the south shore of Long Island.

The relationship of ring number and fork length for each year was best described by the following equations: $Y = 132.308X - 29.890$ in 1985 and $Y = 95.532X + 1.186$ in 1986, where X is log fork length and Y is the number of rings (Fig. 9). The slopes of these regressions differed significantly (ANCOVA, $P < 0.001$). Total otolith length and fork length were highly correlated ($r > 0.99$) and increased isometrically. Total otolith length and ring number also had a high correlation ($r = 0.91$).

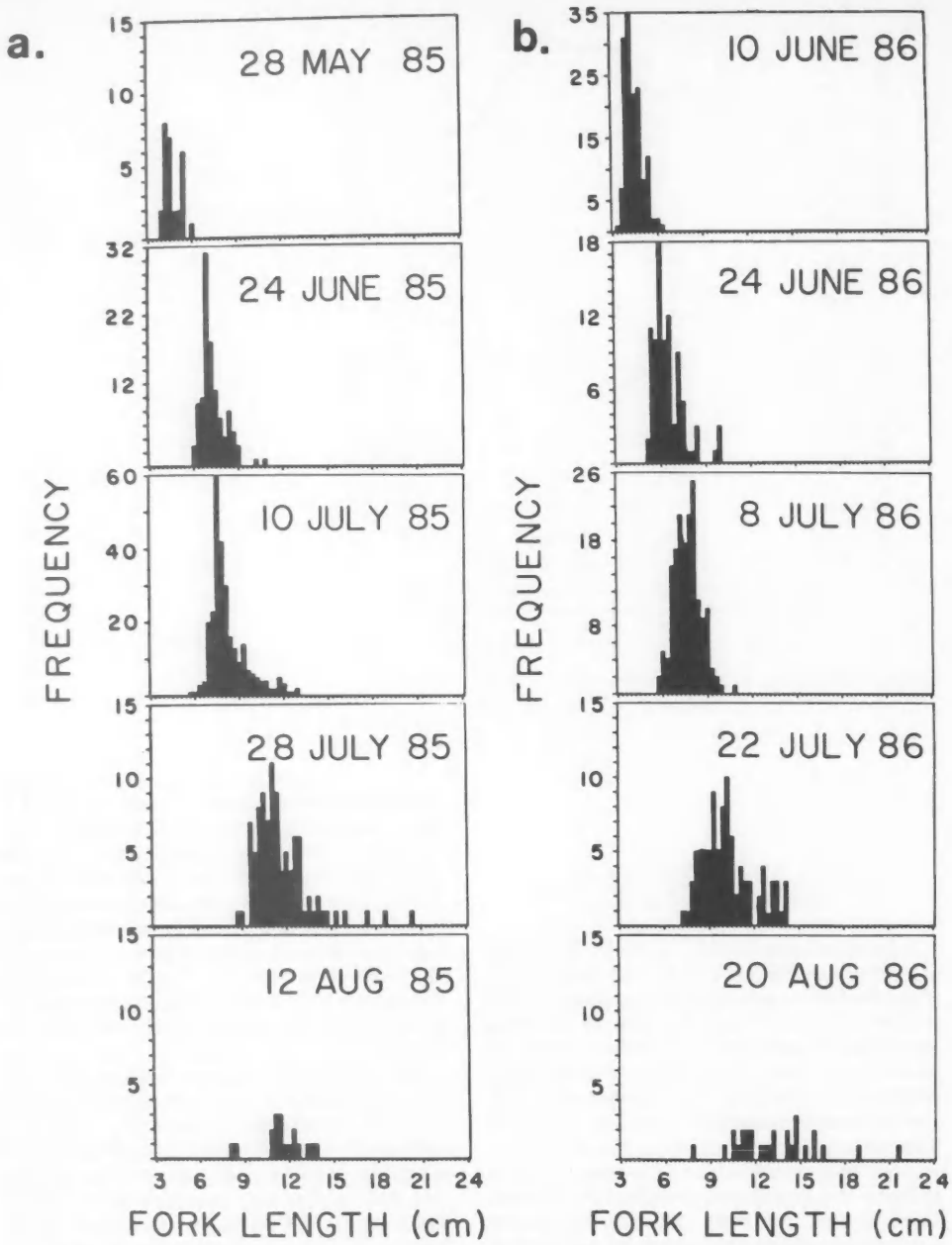

FIGURE 3.—Length-frequency histograms for YOY bluefish (no.) from Great South Bay, NY. (a) 1985; (b) 1986.

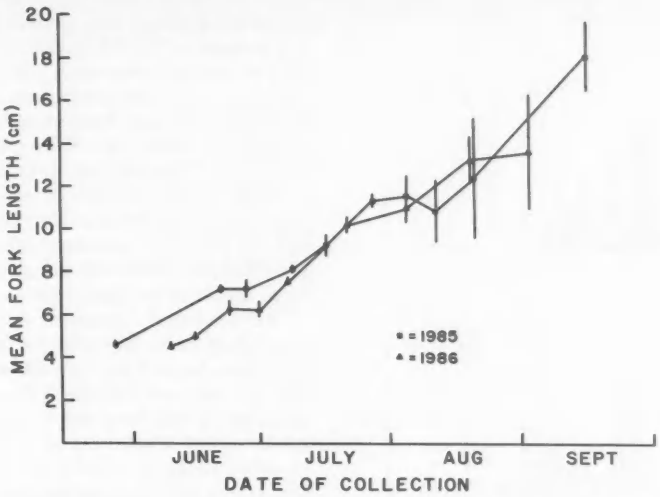

FIGURE 4.—Mean fork length (cm) of YOY bluefish (no.) captured with a beach seine in Great South Bay in 1985 and 1986. Vertical bars are 95% confidence intervals. The last sample in 1986 was caught by angling.

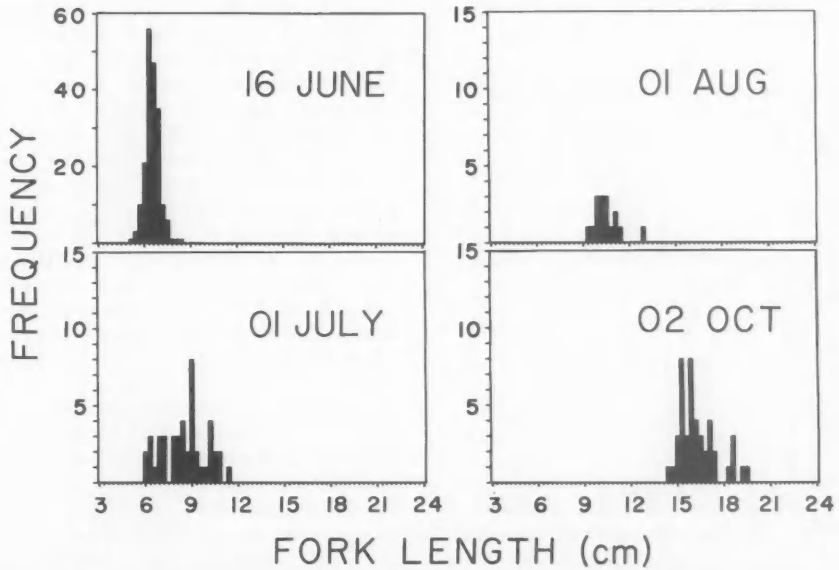

FIGURE 5.—Length-frequency distributions for YOY bluefish (no.) from Jamaica Bay, NY, 1986.

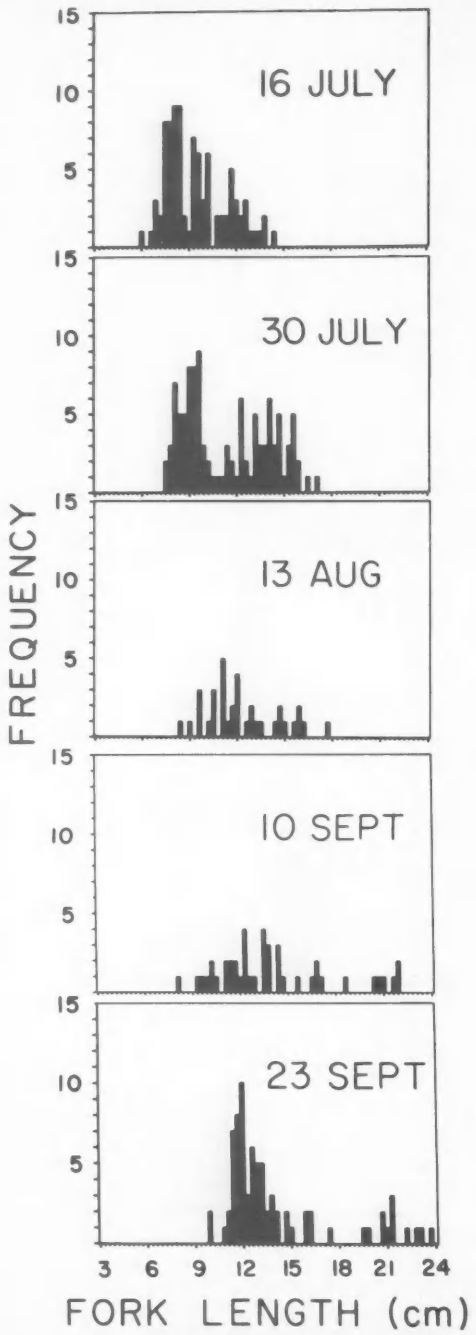

FIGURE 6.—Length-frequency distributions for YOY bluefish (no.) from the Hudson River, NY, 1986.

The analysis was then expanded to the remaining samples of YOY bluefish from Great South Bay that had not been aged. The above length-age equations were used to estimate date of first ring deposition from the dates of capture for all YOY captured in each year of sampling from Great South Bay. This exercise revealed that the vast majority of YOY bluefish in our collections from Long Island had dates of first ring deposition in late March, April, and early May (Fig. 10). The weighted mean date of first ring deposition was 8 April 1985 and 14 April 1986.

The age-length equations for YOY bluefish from Great South Bay were not applied to collections from Jamaica Bay or the Hudson River. Preliminary analyses suggested that the age-length equation for fish from the Hudson River differs substantially from those in Great South Bay, probably owing to a difference in growth rate. Geographic variation in the pattern of recruitment and in the age-length relationships of YOY bluefish are being further investigated.

DISCUSSION

Recruitment of YOY Bluefish to New York

In both 1985 and 1986, the arrival of YOY bluefish on the south shore of Long Island was abrupt. Within about a 1-wk period, CPUE went from 0.0 to 14–18 fish/seine haul. CPUE then remained high for the next two months until declining in August and September when the fish probably became too large to be efficiently sampled by our techniques. These data suggest that the YOY bluefish recruit to the shore zone as a sudden pulse. The timing of this recruitment event is apparently variable, differing by about two weeks among the two years of our study. The appearance of fish 3–6 weeks earlier on the south shore (Great South Bay) than on the north shore (Setauket Harbor) of Long Island suggested that these fish arrive from offshore waters to the south.

Temperature probably influenced the time of arrival of YOY bluefish in the shore zone. In both years of our study, YOY bluefish appeared as temperatures reached about 20°–24°C. In October, after temperatures dropped to the middle

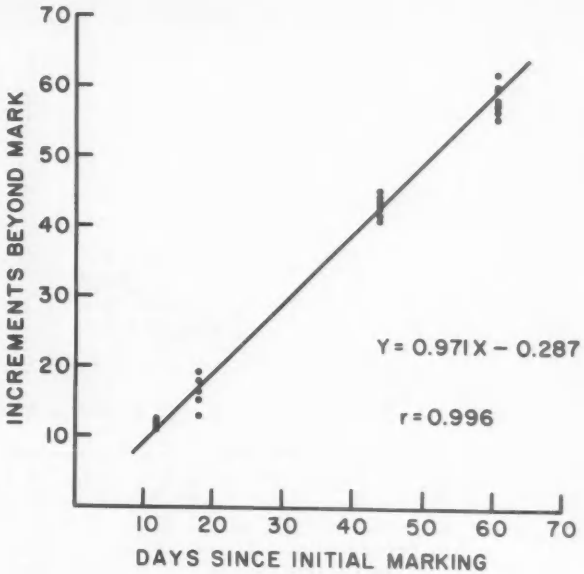

FIGURE 7.—Relation between number of days since marking with tetracycline and the number of growth increments beyond the mark in YOY bluefish maintained in a field cage.

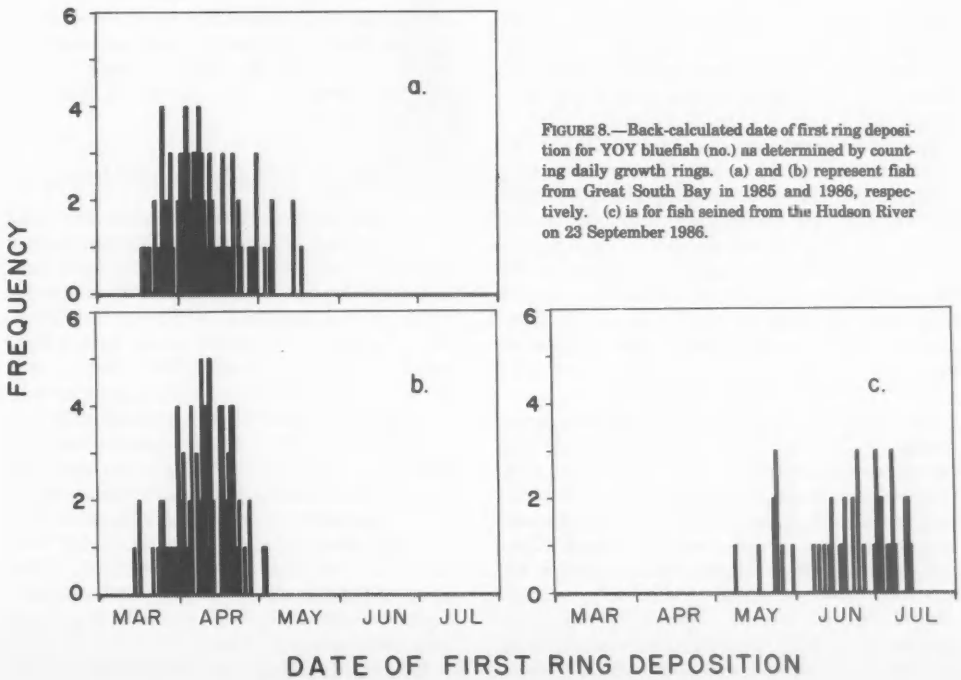

FIGURE 8.—Back-calculated date of first ring deposition for YOY bluefish (no.) as determined by counting daily growth rings. (a) and (b) represent fish from Great South Bay in 1985 and 1986, respectively. (c) is for fish seined from the Hudson River on 23 September 1986.

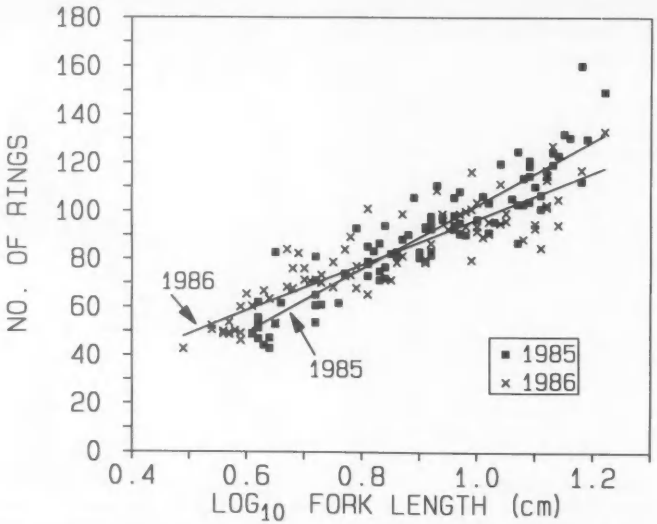

FIGURE 9.—Relation between log fork length (X) and number of otolith rings (Y) for YOY bluefish from Great South Bay, NY. The regression equations are $Y = 132.308X - 29.890$ ($n = 88$) for 1985 and $Y = 95.532X + 1.186$ ($n = 81$) in 1986.

teens, we no longer captured YOY bluefish. Oben (1957) noted that in the Black Sea, YOY bluefish appeared in the shore zone at temperatures of 18°–24.5°C, and left the shore zone in October and November when temperatures dropped to 13°–15°C.

Length-frequency distributions of YOY bluefish from the south shore samples showed only a single mode that attained progressively larger size through the summer and fall, and corresponded to the initial recruitment of fish. If multiple spawning and recruitment events contributed YOY bluefish to Long Island, multimodal length-frequency distributions should have been observed. The unimodal distributions suggested that only one spawning period contributed the majority of YOY bluefish to Long Island.

Interannual variation in the length-age relationship of YOY bluefish was observed. Although recruitment occurred two weeks earlier in 1985 than in 1986, the empirical mean lengths at recruitment were similar (Fig. 4). Postrecruitment growth, however, was slower in 1985 than 1986 so that empirical mean lengths became similar by mid-July. Correspondingly, the slope of the length-age regressions differed significantly among years: YOY bluefish at an age of about 50–70 days had greater fork lengths in 1985 than in 1986 (Fig. 9), but the reverse was true among older, larger fish. Apparently, the growth rate of YOY bluefish prior to recruitment was higher in 1985 than 1986, but this pattern among the two years was reversed during the period of postrecruitment growth.

Validation of Daily Otolith Rings

Our experimental results demonstrate that otolith ring deposition is daily in YOY bluefish. A regression slope of 0.971 indicates a one-to-one correspondence between number of days after injection and the number of rings beyond the tetracycline mark. This outcome is not particularly surprising because numerous studies have shown that increment production is daily, particularly in the early life history when somatic growth is rapid (Brothers et al. 1976; Campana and Neilson 1985; Jones 1985). Cases where ring periodicity is reportedly less-than-daily have involved suboptimal growing conditions (Geffen 1982, 1987; Rice et al. 1985). In our study, the confinement of YOY bluefish in a field cage apparently had little effect on growth rate, or the production of daily growth increments. The field cage allowed for natural light, temperature, and salinity variations that the fish would normally have experienced in na-

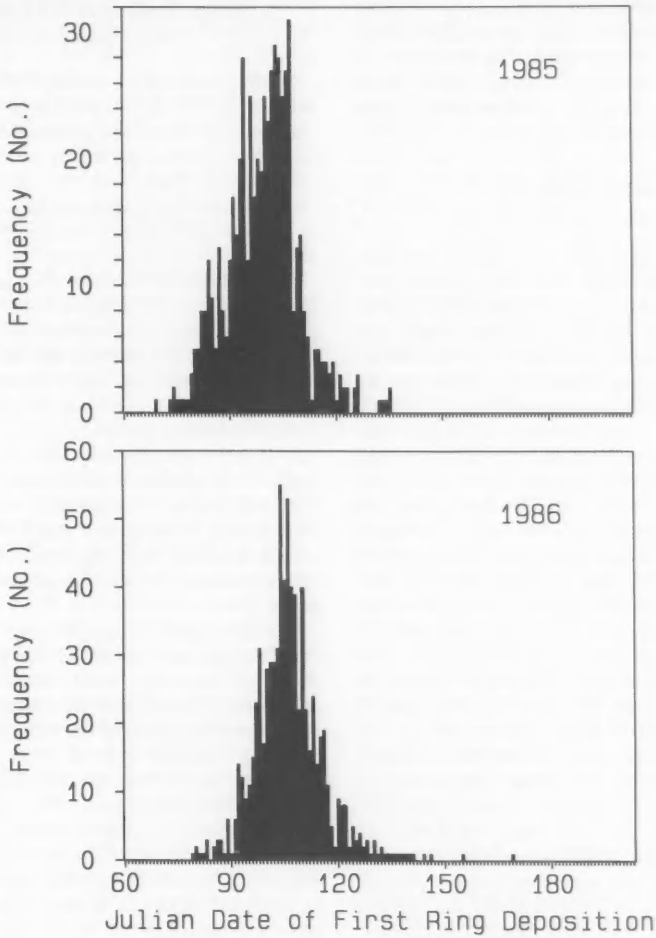

FIGURE 10.—Estimated date of first ring deposition for all YOY bluefish caught in Great South Bay in 1985 (n = 561) and in 1986 (n = 858) using the respective age-length equations in Fig. 9.

ture. Feeding periodicity was probably the primary artifact of confinement that could have affected the rate of ring production in caged fish. However, Marshall and Parker (1982) showed that feeding periodicity did not significantly affect ring production in sockeye salmon, *Oncorhynchus nerka*.

We were unable to determine directly the number of days between spawning and first ring deposition because numerous attempts to capture running-ripe females for initiating experiments on eggs and larvae were unsuccessful. However, most species of fish deposit the first daily growth increment within a few days of hatching (Brothers et al. 1976; Radtke and Dean 1982; McGurk 1984; Radtke 1984; Davis et al. 1985). Recent evidence suggests this is also true in bluefish. Larvae captured off Long Island in 1987 had about seven otolith increments at a total body length of 4–5 mm (R. K. Cowen and D. O. Conover, unpubl. data). Based on the rate of development at 20°C in the laboratory observed by Deuel et al. (1966),

larvae would reach this size in about 5–7 days posthatch. If so, first ring deposition would roughly coincide with hatching. Bluefish hatch in 48 hours at 20°C (Deuel et al. 1966), so the day of first ring deposition probably follows the date of spawning by about 2–4 days.

Spawning Seasons Along the Atlantic Coast

Published studies of larval bluefish distributions along the Atlantic coast suggest the existence of three temporally and spatially distinct spawning seasons: spring and fall spawning seasons in the South Atlantic Bight and a midsummer spawning in the Middle Atlantic Bight. In the only synoptic study covering most of the U.S. east coast, Kendall and Walford (1979) described two periods of high larval abundance: One peak occurred in March and April on the outer shelf of the South Atlantic Bight, and the other peak was in July and August midway over the continental shelf of the Middle Atlantic Bight. Subsequently, Powles (1981) and Collins and Stender (1987) also found the highest abundance of bluefish larvae in the South Atlantic Bight (Cape Canaveral to Cape Fear) to be in April and May. Collins and Stender, however, noted the existence of a lesser peak in larval abundance during September–November. This fall spawning season in the South Atlantic Bight was further confirmed by Finucane and Collins (in press) based on the gonad condition of bluefish from Georgia and the Carolinas. In the Middle Atlantic Bight off Virginia, Norcross et al. (1974) found that eggs and larvae of bluefish first appeared in June, peaked in abundance in July, and persisted into August. Similar observations on the timing of the summer spawning season in the Middle Atlantic Bight were presented by Sherman et al. (1984) and Morse et al. (1987).

Lassiter (1962) provided additional evidence of the existence of relatively discrete spawning seasons in bluefish. He showed that the distribution of back-calculated lengths at age one has a distinctly bimodal pattern among adult fish from North Carolina. Size at age 1 tended to be either about 14 cm or 28 cm. Lassiter showed that the bimodal pattern could not be explained as a difference in growth rate, and suggested that there must be two distinct spawning seasons such that one group of fish had a first growing season about twice as long as the other.

Spawn Dates of YOY Bluefish from New York

Back-calculation to the day of first ring deposition for YOY bluefish recruiting to Great South Bay in 1985 and 1986 demonstrated that these fish were spawned primarily in March and April (Figs. 8, 10). Fish that were spawned in July–August were rarely captured by us on Long Island in 1985 or 1986, despite continued sampling into October.

Recruitment to Jamaica Bay and the Hudson River in July and August 1986 involved YOY bluefish of about the same size as those from Great South Bay. Though the size range of fish from the Hudson was slightly greater than those from Long Island, fish aged from each of the two modes appearing in the July Hudson River samples (Fig. 6) were all spawned during April within about three weeks of each other. The apparent bimodality in July is probably a sampling artifact. Hence, Jamaica Bay and Hudson River fish collected in July and August can be attributed to the same spawning season as those from Great South Bay.

Length-frequency distributions from the Hudson River in September, however, contained a group of unusually small bluefish, and back-calculation showed that they were spawned predominately in June and July (Fig. 8c). These fish probably resulted from the summer spawning season in the Middle Atlantic Bight. Examination of gonads from adult fish captured during 1986 suggested that the running-ripe males and mature females were most abundant during late June and July off Long Island (L. Chiarella and D. O. Conover, unpubl. data). Hence, at least, some summer-spawned YOY bluefish do recruit to the shore zone of the Middle Atlantic Bight. They were, however, much less abundant than spring-spawned YOY bluefish in our 1985 or 1986 samples.

Spawning by bluefish in the spring is known to occur only in the South Atlantic Bight (Kendall and Walford 1979; Collins and Stender 1987). Water temperatures over the shelf north of Cape Hatteras are probably too low for bluefish to spawn in March and April: average shelf water temperatures in the Middle Atlantic Bight range from 5° to 14°C in March and April (Ingham 1986). Virtually no eggs and larvae (Morse et al. 1987) and comparatively few adult bluefish (Gilmore 1985) are captured in plankton or trawl surveys north of Cape Hatteras in March and

April. Moreover, the time of arrival of YOY bluefish on Long Island actually precedes the summer spawning season in the Middle Atlantic Bight. We therefore conclude that YOY bluefish recruiting to the Middle Atlantic Bight in late spring come from spawnings in the South Atlantic Bight.

Larval Transport

The physical mechanisms that account for the transport of bluefish larvae from the South Atlantic Bight to New York are not clear. Spawning in the South Atlantic Bight occurs primarily over the outer half of the continental shelf (Powles 1981; Collins and Stender 1987), and some larvae may be entrained by the Gulf Stream and carried northward into the slope waters of the Middle Atlantic Bight (Kendall and Walford 1979). Neuston net collections in April have shown that bluefish larvae are periodically abundant on both sides of the Gulf Stream-shelf water interface off Cape Hatteras (Kendall and Walford 1979). Collins and Stender (1987) found a negative correlation between larval size and latitude in the South Atlantic, but their sampling may not have extended far enough north (i.e., they did not sample above Cape Fear).

If the Gulf Stream is responsible for the northward transport, a mechanism by which larvae avoid being advected too far offshore would appear to be necessary. According to our results, the interval between spawning and recruitment to Long Island is about 45–60 days, whereas the surface flow of the Gulf Stream at lat. 36°N is about 104 km/day (Iselin 1936). Hence, larvae remaining in the Gulf Stream for an extended period would be transported far off the shelf. Retention near the shelf could be achieved by entering the slope waters at an appropriate time.

The abrupt appearance of YOY bluefish in the shore zone suggests that the onshore migration is a temporally distinct event, perhaps triggered by vernal warming of the shelf. Because the circulation of the slope and shelf waters of the Middle Atlantic Bight is toward the southwest (Sherman et al. 1984), the cross-shelf migration must to some extent involve active swimming.

Very few summer-spawned YOY bluefish were captured in our study. This may not be surprising, however, because the prevailing currents over the midshelf off Long Island would carry larvae to the southwest. If so, summer-spawned fish would be found along the coast from approximately New Jersey to Cape Hatteras. We caution, however, against any general conclusion concerning the lack of summer-spawned fish in New York. There could, for example, be substantial year-to-year variation in the recruitment level of spring- and summer-spawned fish along any particular segment of the U.S. coast. These issues are now being examined by extending our sampling to southern latitudes.

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LITERATURE CITED

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish and Wildlife Service, Fish. Bull. 53:1–577.

BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1–8.

CAMPANA, S. E., AND J. D. NEILSON.
1982. Daily growth increments in otoliths of starry flounder (*Platichthys stellatus*) and the influence of some environmental variables in their production. Can. J. Fish. Aquat. Sci. 39:937–942.
1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014–1032.

COLLINS, M. R., AND B. W. STENDER.
1987. Larval king mackerel *Scomberomorus cavalla*, Spanish mackerel (*S. maculatus*), and bluefish (*Pomatomus saltatrix*) off the southeast coast of the United States, 1973–1980. Bull. Mar. Sci. 41:822–834.

DAVIS, R. D., T. W. STORCK, AND S. J. MILLER.
1985. Daily growth increments in the otoliths of young-of-the-year gizzard shad. Trans. Am. Fish. Soc. 114:304–306.

DEUEL, D. G., J. R. CLARK, AND A. J. MANSUETI.
1966. Description of embryonic and early larval stages of bluefish, *Pomatomus saltatrix*. Trans. Am. Fish. Soc. 95:264–271.

FINUCANE, J. H., AND L. A. COLLINS.
In press. Reproductive biology of bluefish, *Pomatomus saltatrix*, from the southeastern United States. Northeast Gulf Sci.

GEFFEN, A. J.
1982. Otolith ring deposition in relation to growth rate in herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*) larvae. Mar. Biol. (Berl.) 71:317–326.
1987. Methods of validating daily increment deposition in otoliths of larval fish. *In* R. C. Summerfelt and G. E. Hall (editors), Age and growth of fish, p. 223–240. Iowa State Univ. Press, Ames.

GILMORE, J.
1985. Oceanic distribution, abundance, and migration of bluefish along the east coast of the United States. M.S. Thesis, State University of New York, Stony Brook, 60 p.

INGHAM, M. C.
1986. Sea surface temperatures in the northwestern Atlantic in 1985. NAFO SCR Doc. 86/75.

ISELIN, C. O'D.
1936. A study of the circulation of the western North Atlantic. Pap. Phys. Oceanogr. Meteorol. 4:1–101.

JONES, C. J.
1985. Determining age of larval fish with the otolith increment technique. Fish. Bull., U.S. 84:91–103.

KENDALL, A. W., JR. AND L. A. WALFORD.
1979. Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. Fish. Bull., U.S. 77:213–227.

LASSITER, R. R.
1962. Life history aspects of the bluefish, *Pomatomus saltatrix* (Linnaeus), from the coast of North Carolina. M.S. Thesis, North Carolina State College, Raleigh, NC, 91 p.

MARSHALL, S. L., AND S. S. PARKER.
1982. Pattern identification in the microstructure of sockeye salmon (*Oncorhynchus nerka*) otoliths. Can. J. Fish. Aquat. Sci. 39:542–547.

MCGURK, M. D.
1984. Ring deposition in the otoliths of larval Pacific herring, *Clupea harengus pallasi*. Fish. Bull., U.S. 82:113–120.

MORSE, W. W., M. P. FAHAY, AND W. G. SMITH.
1987. MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia (1977–1984). Atlas No. 2. Annual distribution patterns of fish larvae. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/NEC-47, 215 p.

NORCROSS, J. J., S. L. RICHARDSON, W. H. MASSMANN, AND E. B. JOSEPH.
1974. Development of young bluefish (*Pomatomus saltatrix*) and distribution of eggs and young in Virginian coastal waters. Trans. Am. Fish. Soc. 103:477–497.

OBEN, L. C.
1957. About the drifting approach of fingerling bluefish (*Pomatomus saltatrix*) (Linnaeus) to the shores of the Black Sea in the Karadaga region (1947–1954). Karadagskaia Biol. Stn. Tr. (4):155–157.

POWLES, H.
1981. Distribution and movements of neustonic young of estuarine dependent (*Mugil* spp., *Pomatomus saltatrix*) and estuarine independent (*Coryphaena* spp.) fishes off the southeastern United States. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:207–209.

RADTKE, R. L.
1984. Formation and structural composition of larval striped mullet otoliths. Trans. Am. Fish. Soc. 113:186–191.

RADTKE, R. L., AND J. M. DEAN.
1982. Increment formation in the otoliths of embryos, larvae and juveniles of the mummichog, *Fundulus heteroclitus*. Fish. Bull., U.S. 80:201–215.

RICE, J. A., L. B. CROWDER, AND F. P. BINKOWSKI.
1985. Evaluating otolith analysis for bloater *Coregonus hoyi*: do otoliths ring true? Trans. Am. Fish. Soc. 114:532–539.

SHERMAN, K., W. SMITH, W. MORSE, M. BERMAN, J. GREEN, AND L. EJSYMONT.
1984. Spawning strategies of fishes in relation to circulation, phytoplankton production, and pulses in zooplankton off the northeastern United States. Mar. Ecol. Prog. Ser. 18:1–19.

U.S. DEPARTMENT OF COMMERCE.
1986. Recreational fishery statistics for 1985. U.S. Dep. Commer., NOAA, NMFS, 130 p.

WILK, S. J.
1977. Biological and fisheries data on bluefish, *Pomatomus saltatrix* (Linnaeus). NMFS, NEFC, Sandy Hook Lab. Tech. Ser. Rep. No. 11, 56 p.

ON THE ROLE OF FOOD-SEEKING IN THE SUPRABENTHIC HABIT OF LARVAL WHITE CROAKER, *GENYONEMUS LINEATUS* (PISCES: SCIAENIDAE)

A. E. JAHN, D. M. GADOMSKI, AND M. L. SOWBY[1]

ABSTRACT

Fish larvae and their prey were sampled from discrete depths within the bottom meter and at middepth near the 15 m depth contour off southern California. The smallest white croaker larvae (<2.7 mm NL) occurred mostly at middepth. Mid-sized larvae (2.7 mm to the beginning of flexion) were almost all collected at the two depths nearest the bottom. All preflexion-stage larvae ate small (50–300 μm in length) prey, chiefly rotifers, copepod nauplii, tintinnids, and invertebrate eggs. Although small and mid-size larvae ate these items in different proportions, this difference could not be ascribed to vertical distribution. Diet of the largest larvae, flexion and postflexion (roughly 5–15 mm), consisted mainly of copepods and differed by >90% from diets of smaller larvae. Though largest larvae were only captured 50 cm above the bottom, their prey, with one exception (amphipods), were more abundant at or above 1 m. It was concluded that the observed suprabenthic concentration of older white croaker larvae was probably not motivated by food-seeking.

Disparity between concentrations of food required for survival and growth of laboratory-reared fish larvae and observations of average concentrations of food organisms in the ocean has led to the widely accepted idea that aggregations of fish larvae and their food must frequently overlap in nature (see reviews by Theilacker and Dorsey [1980] and Hunter [1981]). Direct and indirect evidence for the importance of overlapping concentrations of larvae and their prey (Lasker 1975, 1978; Govoni et al. 1985; Buckley and Lough 1987) comes from sampling at fronts and discontinuities in the pelagic environment. One interface that attracts many zooplankters is the seabed itself (Hamner and Carleton 1979; Wishner 1980; Sainte-Marie and Brunel 1985). On the southern California continental shelf, the seabed serves as a surface of aggregation for larvae of numerous fish species (Brewer et al. 1981; Schlotterbeck and Connally 1982; Barnett et al. 1984; Jahn and Lavenberg 1986) and other zooplankton (Clutter 1969; Barnett and Jahn 1987) and of large-zooplankton biomass (Jahn and Lavenberg 1986). While it is tempting to suggest a trophic advantage to the suprabenthic habit of the fish larvae, near-bottom concentrations of organisms actually eaten by larval fishes have yet to be demonstrated along the open coast.

In all cases reported, concentration in the near-bottom zone was greater in older larvae and, when observations permitted, greater during the day than at night (Brewer and Kleppel 1986; Jahn and Lavenberg 1986). The phenomenon is therefore thought to be behavioral. Possible advantages of such behavior, including avoidance of midwater predators, maintenance of position on the shelf, and increased encounters with high concentrations of food, have been discussed elsewhere (Barnett et al. 1984; Brewer et al. 1984; Brewer and Kleppel 1986; Jahn and Lavenberg 1986). In discussing the near-bottom schooling behavior of a larval clupeoid in Japan, Leis (1986) stated, "knowledge of the biology of epibenthic fish larvae is too rudimentary to allow a clear assessment of the advantages and disadvantages. . . ." Whatever the advantages, a seemingly more answerable question about the near-bottom habit is what causes the larvae to behave as they do? In another study from Japan, Tanaka (1985) showed that juvenile red sea bream, *Pagrus major*, exploited suprabenthic copepod populations, and he speculated that the distribution of prey was a template for the descent of the fish from midwaters and its subsequent migration into estuaries. The question addressed in the present study was whether the fine-scale layering of larval fishes was a direct response to that of their prey field.

Because of the immediate behavioral aspect of

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the question posed, a 1-d study was thought appropriate. Though environmental conditions on this day might differ from "average", fish larvae were assumed to be capable of a constant array of behaviors. In other words, response (if any) of the larvae to the vertical distribution of their prey was assumed to be a deterministic rather than a statistical phenomenon. If their vertical distribution resembled that of their prey, then food-seeking would remain a plausible explanation for the near-bottom habit; if not, then other stimuli must be considered important in shaping these near-bottom concentrations of fish larvae.

The sampling was planned for daylight hours, when most feeding by larvae was expected to occur (Hunter 1981; Govoni et al. 1983). Late winter was chosen because in this season peak larval abundances of several species of interest to us (northern anchovy, *Engraulis mordax*; white croaker, *Genyonemus lineatus*; California halibut, *Paralichthys californicus*; and sometimes queenfish, *Seriphus politus*, often overlap (Lavenberg et al. 1986). A survey cruise in late February found moderate-to-high abundance of the first three species plus California sardine, *Sardinops sagax*, (all >0.2 m^{-3}, Lavenberg unpubl. data), and so this study was scheduled for 19 March 1985 off Seal Beach, CA (lat. 33°41′N, long. 118°05′W; for a map, see Jahn and Lavenberg 1986).

As it happened, we chanced to encounter conditions that were less typical than those found on the February cruise. Only one fish species, white croaker, was abundant enough to merit analysis, and an uncommonly reported prey item, rotifera, was important for small larvae. The diet of various-sized larvae with respect to the abundance of prey organisms at an array of heights above the seabed was nevertheless useful in questioning whether food-seeking shaped the observed larval distribution.

METHODS

Field

At the hour of 0750 PST, an array of Interocean model S4[2] electromagnetic current meters was set out over the 15 m isobath, with current meters 1, 4, and 8 m above the seabed. These meters were set to record average current vectors and temperature at 5-min intervals. The vessel (RV *Westwind*) was then anchored some 200 m seaward of the current meter array. A Nielson model NCH fish pump, rated at 227 m^3 h^{-1} at a 2 m head, was used to sample fish larvae and zooplankton. The end of the hose was tethered between a 200 kg flat steel weight and several subsurface floats, with a pulley arrangement such that divers could adjust the distance between hose mouth and seabed. A similar setup was previously found to give repeatable, fine-scale resolution at vertical separations of 25 cm (Jahn and Lavenberg 1986). Sampling heights above the bottom were 50 cm, 1 m, and 6.7 m. The 15.2 cm diameter hose was nearly horizontal at the tether point, so that nominal sampling strata were $z \pm 7.6$ cm. Vessel surge, transmitted through the stiff hose, caused occasional downward excursions of some 10 cm.

Accompanying each pump sample was a cast of water bottles for phytoplankton and microplankton analysis. Rigid arrays of horizontally held 4 L Niskin bottles (cf. Owen 1981) were used to take water samples simultaneously from 25, 50, and 100 cm above the bottom. The bottle array was designed to be tripped by messenger, but poor performance led to diver-implemented use after the second cast. A midwater sample, 7.5 m below the surface, was obtained via a single Niskin bottle for each sample set.

The sampling plan thus consisted of duplicate pump samples from each of three strata, each pump sample to be accompanied by a set of bottle samples from four standard heights, three within 1 m of the seabed and one at midwater column. One-liter samples from the bottles were fixed in Lugol's solution for later identification of phytoplankton and microplankton. Pump samples of 15-min duration (approximately 35 m^3) were mainly directed into an overboard, 330 μm mesh plankton net for retention of large zooplankton and ichthyoplankton. Unexpected problems in reading an inline flowmeter required that volumes be estimated as 2.4 m^3 min^{-1}, based on previous experience with the pump under similar conditions aboard the same vessel. To collect smaller zooplankton, a 5 cm diameter hose led from the intake side of the fish pump to a 100 μm mesh plankton net. This small-meshed net was suspended over a watertight box, which was marked such that exactly 0.5 m^3 could be subsampled for animals too small to be quantitatively retained by the large net. This subsample, which

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

was first seived through 330 μm mesh, took about 10 minutes to obtain; the portion retained on the 330 μm mesh was added to the contents of the large plankton net. All pump samples were preserved in 5% formalin.

Laboratory

All fish larvae and eggs were sorted from the large zooplankton samples and identified. All specimens of white croaker, the only species abundant in all six collections, were measured with an eyepiece micrometer in units of 0.024, 0.062, or 0.159 mm, depending on magnification. Length was measured from tip of snout to end of straight (NL) or flexed (FL) notochord or to the end of the hypural plate when this margin was vertical (SL). A further designation of developmental stage indicated the amount of yolk present: "free embryos" (Balon 1975) had a relatively massive yolk sac and may or may not have had functional eyes and mouths; more advanced individuals with a much-reduced or totally resorbed yolk sac, fully pigmented eyes, and an apparently functional mouth were designated "feeding-stage" larvae, or simply "larvae".

All larvae, plus a maximum of 20 free embryos with apparently functional mouths from each collection, were dissected for gut contents analysis by methods described in Arthur (1976) and Gadomski and Boehlert (1984). Length, rather than width, of prey items was measured, because it was considered a more conservative property of often crushed specimens and because our concern was not so much with what the larvae *could* eat (Hunter 1981) as with what they *did* eat. Lengths of prey items (of copepods, cephalothorax length) were recorded in 50 μm classes up to 200 μm, by 100 μm classes from 200 μm to 1 mm, and by 0.5 mm classes at larger sizes. In a few cases, these size categories were inconvenient, and more inclusive ranges were used.

Water bottle samples of phytoplankton and microzooplankton were prepared following procedures in Utermöhl (1931). From a thoroughly agitated sample, a 50 mL subsample for net phytoplankton was taken and placed in a settling chamber overnight (about 14–18 hours). Cells were identified and counted in 10 ocular fields, and mean density (cells per liter) calculated as the number counted scaled by the proportion of the area of the 10 fields (20.6 mm^2 total) to the area of the slide (510.7 mm^2).

Microzooplankton was filtered from a 500 mL subsample onto a 35 μm mesh screen, washed from the screen into a 50 mL settling tube and allowed to settle overnight. All organisms >50 μm were counted and identified to taxon and size category, using the same system as for larval fish gut contents. Densities were scaled to number per liter.

The 100 μm zooplankton samples were concentrated to 200 mL, then subsampled twice using a 10 mL Stempel pipette. Organisms were identified and classified to size categories as described above for larval fish prey. Counts from two subsamples were averaged and expressed as number per m^3.

Data Analysis

The microzooplankton (from water bottles) data set consisted of six vertical profiles of four sampling heights each. Principal components analysis was used to look for vertical layering and time-correlated changes in the makeup of these assemblages. A list of taxa present in three or more samples from at least one sampling height was chosen. Abundances were log-transformed $[\log_{10}(x + 1)]$, and principal components computed from the covariance matrix. Component scores for each of the 24 samples were used to make plots in which two- and three-dimensional groupings were sought that could be clearly related to sampling height or to the sequence in which the samples were taken. The taxa having high loadings on axes (components) identified with time and vertical trends were subsequently scrutinized individually. A similar analysis was done for phytoplankton, but omitted here in the interest of brevity.

Gut contents were conveniently analyzed by lumping taxa into the 10 categories: dinoflagellate, tintinnid, rotifer, polychaete larva, lamellibranch larva, crustacean nauplius, copepodite and adult copepod, amphipod, invertebrate egg, and "other". Unidentifiable matter was ignored in all comparisons. To test for differences in diet between subsets of larvae, we used an adaptation of the "bootstrap" (Efron 1982). The test criterion was the percentage of prey comprised by a major item in one of the two groups of guts. The null hypothesis that two sets were not different was simulated by combining the two data sets and then, through repeated sampling, determining the probability of observing the criterion percentage from such a mixture.

RESULTS

General Observations

The water column was very weakly stratified, with temperatures of 12.9 ± 0.1°C at 1 m, 13.0 ± 0.2°C at 4 m and 14.1 ± 0.1°C 8 m above the bottom during the time of biological sampling. Near the bottom, a turbid suspension limited visibility to arm's length; the surface of the sediment was never clearly seen on any of the seven descents during the hours of 0930–1630. The midwaters below about 3 m from the surface were densely populated with larvaceans (visually estimated and later confirmed to be about 10 L^{-1}). Total diatom cell counts (principally *Nitzschia* spp.) were of order 10^5 L^{-1} in all samples, bloom quantities suggestive of recent upwelling (cf. Tont 1981).

Currents and Plankton

During the hours of biological sampling, currents ran steadily alongshore to the southeast, being deflected counterclockwise near the bottom and ranging from about 14 cm s^{-1} at 8 m to 6 m s^{-1} at 1 m above the seabed. At these current speeds, one may expect that the approximately 5-h period from beginning to end of biological sampling should correspond to a minimum spatial spread of 1–2.5 km. Distances of this order were previously found to be an important length scale of variation in larval fish abundance (Jahn and Lavenberg 1986). Because the spatial dimension of interest regarding distribution of larval fish prey was the vertical, we needed to quantify, at least partially, the effects of time (vertical migration?) and distance (advection) on the composition and vertical dispostion of the plankton.

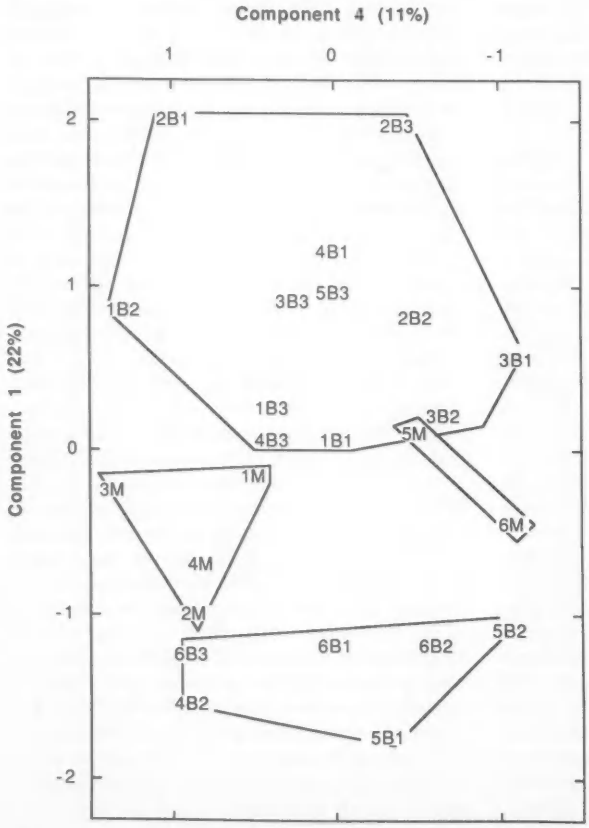

FIGURE 1.—Projections of microzooplankton samples onto the first and fourth principal component axes. The initial digit represents profile number, M = midwater, B = near-bottom, final digit is proximity to bottom (1 = 25 cm, 2 = 50 cm, 3 = 100 cm), see Figure 3.

Accordingly, the microplankton data set, representing six vertical profiles separated in time, was reduced to principal components for examination of possible time effects.

Twenty-four taxonomic/size categories of microzooplankton were used to compute principal component scores for the 24 samples. The first four principal components accounted for 60% of the variance. No clear separation of midwater from near-bottom samples was seen. The first component, which accounted for 22% of the variance, separated the near-bottom samples into two groups, morning to midday and afternoon (Fig. 1), leaving the midwater samples at intermediate projections. The midwater samples were in turn separated by the fourth component (11% of the variance) into time groups corresponding to those of the near-bottom set. No stratification by sampling height was seen within the near-bottom samples, and none of the other axes provided separation by time. The highest loading variables on components 1 and 4 (Table 1) were various sizes of rotifer and, for component 1, three genera of tintinnids (*Favella*, *Acanthocystis*, and *Dadayella*). Much of the time-correlated variance structure depicted in Figure 1 thus appears to be due to change in the size composition of rotifers, described in a later section, and a decrease in these three tintinnids near the bottom in late afternoon (Table 2). An identical analysis of the phytoplankton data found no trends in time or depth.

TABLE 1.—Loadings of important variables on the first and fourth principal components of microplankton data.

Component 1		Component 4	
Variable	Loading	Variable	Loading
Rotifer		Rotifer, 100–150 μm	0.388
150–200 μm	0.572		
200–300 μm	−0.380	Egg, 50–100 μm	0.349
Tintinnids		Copepod nauplii,	
Favella sp.	0.365	150–200 μm	−0.252
Acanthocyctis sp.	0.331		
Dadayella sp.	0.314		

Larval Fish Abundance

Of 1,125 total fish larvae taken in the six pump samples, 666 (59%) were white croaker, a deep-bodied, robust larva (Watson 1982). More than half (338) of these had absorbed the yolk sac and were thus of feeding size. The second most abundant feeding-stage larva was an unidentified gobiid type (84 specimens), but this taxon was not taken above 100 cm of the seabed and so was excluded from the gut analysis. Feeding-stage California sardine, northern anchovy, and California halibut—all relatively abundant (>0.2 m^{-3}) in the area three weeks earlier—each represented <1% of the catch. Although the earlier survey employed oblique bongo net tows, past comparison of the Nielsen pump with bongo tows found no significant differences in diversity or abundance estimates based on similar-volume samples (R. Schlotterbeck[3]). We therefore think the differences between the February survey and our March samples were due mainly to a real change in the ichthyoplankton, from a typical late winter assemblage (McGowen 1987; Walker et al. 1987) to a more depauperate one.

Vertical Distribution and Feeding Incidence of Larval White Croaker

White croaker free embryos ranged in abundance from <0.1 m^{-3} at 0.5 m to ≈1 m^{-3} at 1 m to >2 m^{-3} at 6.7 m above the bottom. Of 61 free embryos dissected, none had gut contents.

Feeding-stage larvae of white croaker were only slightly more abundant at 6.7 m (1.9–2.2 m^{-3}) than at 1 m and 0.5 m (1.1–1.6 m^{-3}), but

[3]R. Schlotterbeck, Robert Schlotterbeck, Inc., 18842 Ridgeview Cr., Villa Park, CA 92667, pers. commun. April 1986.

TABLE 2.—Density (cells per liter) of three tintinnids as a function of time and sampling height. Each set of three numbers gives the density of *Favella* spp. (F), *Acanthocystis* spp. (A), and *Dadayella* spp. (D).

Height	Time (PST)																	
	1030			1130			1220			1313			1425			1454		
(cm)	F	A	D	F	A	D	F	A	D	F	A	D	F	A	D	F	A	D
750	6	4	20	0	4	22	0	4	12	2	0	12	46	12	14	42	6	18
100	2	4	24	30	18	24	6	18	48	0	2	26	8	4	24	0	0	26
50	0	6	18	26	12	44	0	2	24	0	0	4	0	0	4	0	6	12
25	2	6	4	14	12	44	0	22	54	10	2	26	0	0	0	0	0	0

there was a marked gradient in development with proximity to the seabed (Fig. 2). All the larvae at 6.7 m had unflexed notochords, and most were <2.5 mm NL. Feeding incidence (proportion of larvae with nonempty guts) was 78% at this height. At 1 m, modal larval length was 2.65 mm, with a single postflexion specimen (Fig. 2); feeding incidence was 74%. At 0.5 m there were still some preflexion larvae, but a second length mode at 6.8 mm represented postflexion-stage larvae. Feeding incidence was 90% at 0.5 m above the bottom, being somewhat greater among flexion

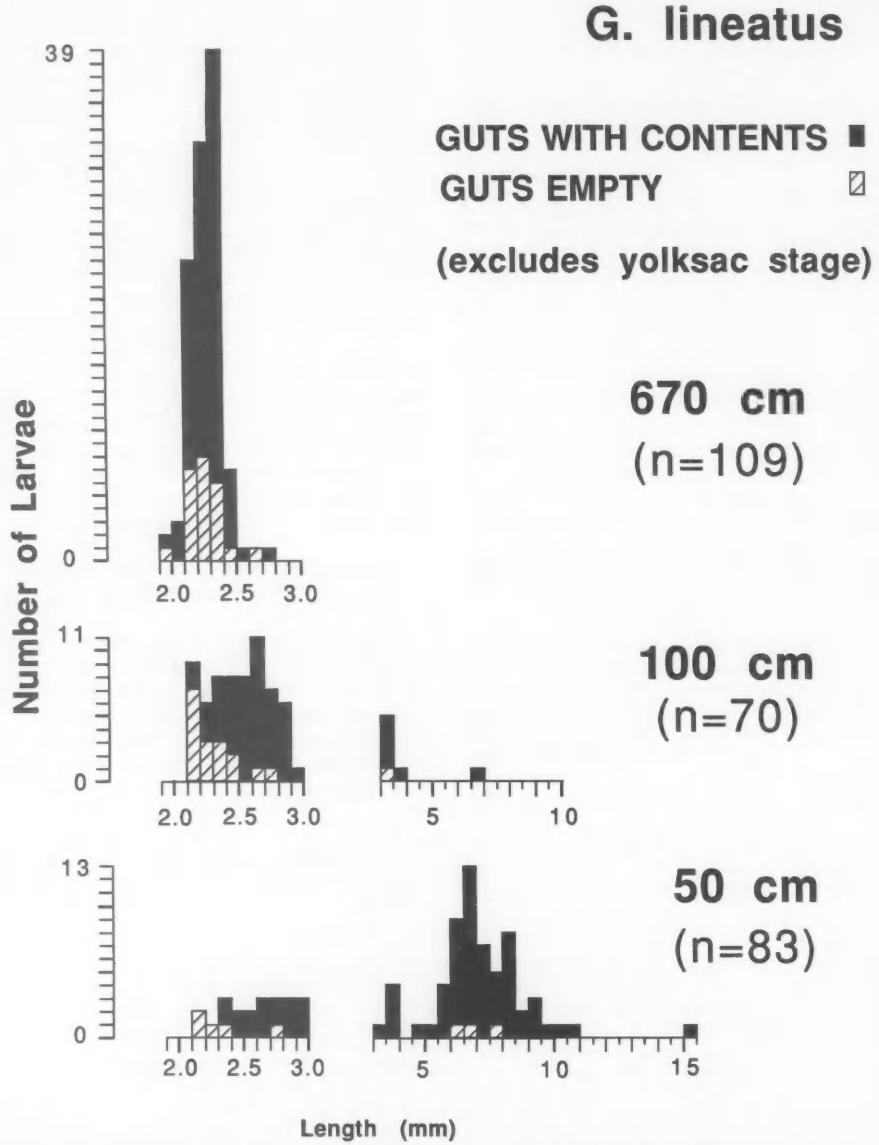

FIGURE 2.—Length frequencies of feeding-stage larvae of *Genyonemus lineatus* at three sampling heights.

and postflexion larvae (95%) than among preflexion larvae (82%).

Gut Contents

The white croaker larvae were divided into three size classes for analysis of gut contents with regard to height above the bottom: preflexion larvae <2.7 mm (size 1), preflexion larvae >2.7 mm (size 2), and flexion and postflexion larvae (size 3). The largest preflexion larva was 4.6 mm NL, and the smallest flexion stage larva was 5.5 mm FL. The division of preflexion larvae at 2.7 mm retained all but one specimen at 6.7 m in size 1 while partitioning the preflexion larvae at 1 m and 0.5 m about equally into sizes 1 and 2 (Figs. 2, 3). Besides the 2.75 mm specimen at 6.7 m, a single flexion stage larva at 1 m was excluded by these criteria from the comparisons.

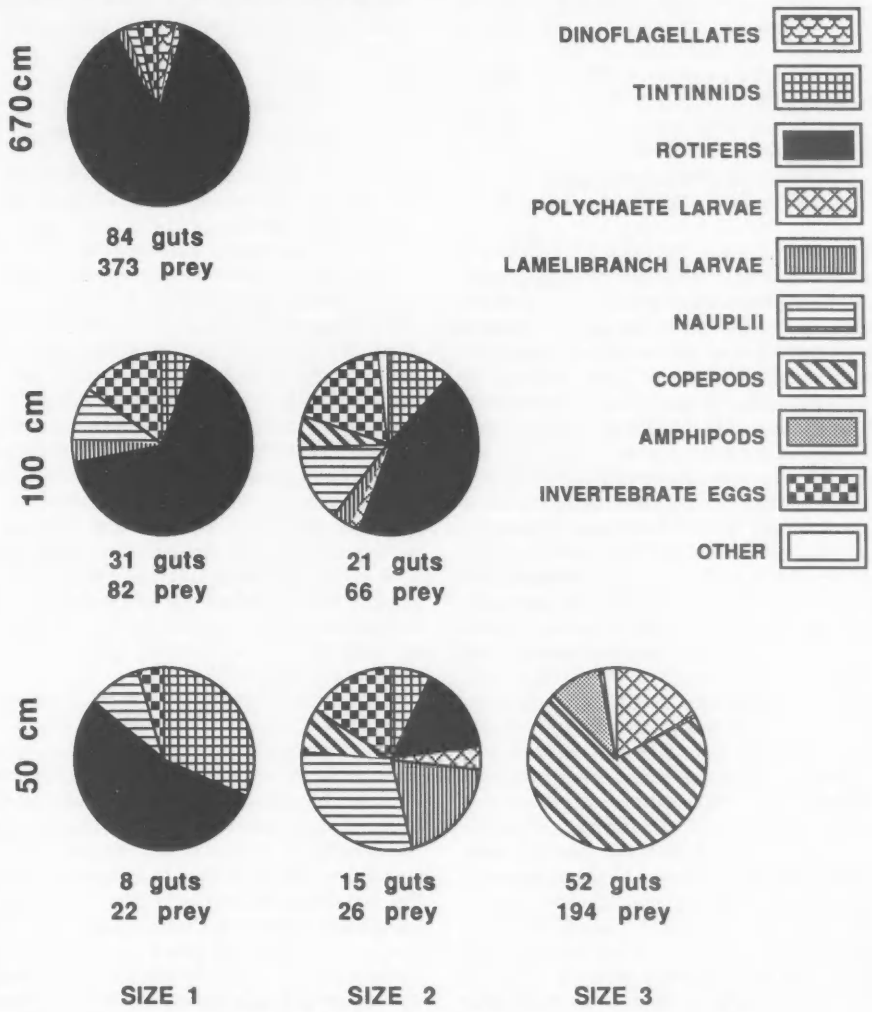

FIGURE 3.—Percentage contribution of 10 food categories to the diet of larval white croaker at three heights above the bottom. Size 1 = preflexion larvae <2.7 mm NL; size 2 = preflexion larvae >2.7 mm NL; size 3 = flexion and postflexion-stage larvae.

Most identifiable prey items fit into the nine categories: dinoflagellate, tintinnid, rotifer, polychaete larva, lamellibranch larva, crustacean nauplius, copepodite and adult copepod, amphipod, and invertebrate egg (Fig. 3). The "other" category applied only to size-2 larvae at 1 m (1 *Globigerina* sp.) and to size-3 larvae (1 zoea, 3 larvaceans, and two large [1 mm] unidentified spheres).

Guts of preflexion (sizes 1 and 2) larvae from the three sampling heights contained an array of small (<300 μm) organisms that varied mainly in proportions from mostly rotifers (88%) in size-1 larvae at 6.7 m to a diverse mix of prey numerically dominated by nauplii in size-2 larvae at 0.5 m (Fig. 3). Percent similarity (overlap) among the 5 groups of preflexion larvae ranged from 24 to 75%. The gut of the single size-2 larva at 6.7 m, not included in Figure 3, contained two tintinnids.

Size-3 larvae had a diet consisting chiefly of copepodite and adult copepods that overlapped only 8–9% with size-2 larvae and 1% or less with the three groups of size-1 larvae. The copepods eaten by size-3 larvae were mostly *Corycaeus anglicus* (62% of all copepods), unidentified copepodites (cyclopoid and calanoid, 25%), and *Paracalanus parvus* (9%). Polychaete larvae were identified only from the presence of setae in the guts, so the proportion (nominally 16% of all prey items) of this taxon in the diet is more an indication of incidence than of numerical importance. Amphipods, mostly in the length range 1–1.5 mm, were found in white croaker larvae ranging from 6.5 mm FL to 10.3 mm SL. The gut of the flexion-stage larva at 1 m, not included in Figure 3, contained three *C. anglicus* and traces of polychaete setae.

While there can be no doubt that flexion and postflexion larvae had a different diet than preflexion larvae, the pattern of decreasing proportion of rotifers with increasing size and proximity to the bottom among preflexion larvae was of questionable statistical significance. The first question asked was whether the very high percentage of rotifers in the diet of size-1 larvae at 6.7 m was likely to have arisen by chance from a random sampling of size-1 larvae. Formally stated, H_0 = "all size-1 larvae had the same percentage of rotifers". The 123 nonempty guts were pooled, and random samples of 84 each were drawn. In 1,000 iterations, <4% of the samples had ≥88% rotifers, so it was concluded that larvae at 6.7 m ate significantly more rotifers than similar-sized larvae near the bottom. The remaining 75 preflexion larvae (sizes 1 and 2) are divided into 4 small groups at 0.5 and 1 m, so we next tested for a size effect by pooling across sampling height, such that the guts of the 39 near-bottom size-1 larvae contained 64% rotifers, and the 36 size-2 larvae had 36% rotifers. Bootstrapping as before, <2% of samples of 36 had ≤36% rotifers, so it was concluded that size-1 and size-2 larvae differed in this regard. Further testing (e.g., of a height effect within sizes) was not done because of small sample sizes and multiple testing considerations.

Abundance and Vertical Distribution of Prey

Rotifers, all identified as the brachionoid *Trichocerca* sp., figured importantly both in the diet of preflexion larvae and in the time-related variance structure of the microplankton. As shown in Table 3, there was a change in the size spectrum of these animals that coincided approximately with the time of changing from near-bottom sampling to midwater sampling with the fish pump. It was only the largest category of rotifer (200–300 μm, including the "toe") that was found in the guts of the larvae. The relative abundance of total rotifers in the plankton at the times and heights of pump sampling differed very little (25–33% of all organisms in the 100–300 μm size class), but the percentage of rotifers in the 200–300 μm class increased from 21% (near-bottom, morning) to 86% of all rotifers (midwater, afternoon). The dominance of rotifers in the diet of size-1 larvae in midwaters is thus likely related to the larger size of rotifer resident in the water column when that height was sampled.

The most notable dietary difference among the larval size groups analyzed was the switch from small (50–300 μm) to larger (0.5–2.5 mm) prey, principally the copepod *Corycaeus anglicus* (0.5–0.8 mm), upon flexion of the notochord. The abundance of *Corycaeus* from the 100 μm mesh pump samples (Table 4) shows that this prey item was equally or more abundant in midwater than near the bottom, where all the flexion and postflexion larvae were captured. (Within the bottom meter, the similar-sized but more transparent *Paracalanus parvus* outnumbered *C. anglicus* by a factor of 5–20.) The only prey found in numbers in these larvae that was restricted to the 0.5 m samples was gammarid amphipods. Larger crustaceans—cumaceans, crab and shrimp zoea,

TABLE 3.—Density (rotifers per liter) of *Trichocerca* sp. as a function of time and sampling height. Each set of three numbers gives the density of 100–150 μm, 150–200 μm, and 200–300 μm rotifers. Height of simultaneous pump sample is given.

Time (PST):	1030			1130			1220		
Pump height:	0.5 m			0.5 m			1 m		
Sampling height (cm)	100–150 μm	150–200 μm	200–300 μm	100–150 μm	150–200 μm	200–300 μm	100–150 μm	150–200 μm	200–300 μm
750	8	0	4	4	0	10	0	0	20
100	8	14	0	0	66	0	14	22	10
50	24	18	0	0	8	40	0	34	0
25	0	2	12	16	46	0	0	30	0
Time (PST):	1313			1425			1454		
Pump height:	1 m			6.7 m			6.7 m		
Sampling height (cm)	100–150 μm	150–200 μm	200–300 μm	100–150 μm	150–200 μm	200–300 μm	100–150 μm	150–200 μm	200–300 μm
750	20	0	0	0	12	14	0	0	60
100	0	4	0	12	24	0	46	0	102
50	6	0	34	0	4	16	0	0	42
25	0	26	0	0	0	6	0	2	0

TABLE 4.—Abundance (animals m^{-3}) of copepodite and adult *Corycaeus* spp. in 100 μm mesh samples from the fish pump.

Height (m)	First sample	Second sample
6.7	1,080	460
1	120	500
0.5	180	140

mysids, and euphausid furcilia larvae—were all abundant (>10 m^{-3}) in the 0.5 m, 330 μm mesh samples but with the exception of the *callianassa* zoea mentioned above (from the gut of an 11 mm larva) were not found in these white croaker larvae.

DISCUSSION

The chief drawback of the pumping system used was its inability to obtain a simultaneous vertical profile. The sampling sequence left the possibility that differences among heights might be confounded by trends in time, as discussed by Jahn and Lavenberg (1986). Slight time effects were found among the vertical profiles of microplankton, increasing the suspicion that the apparent vertical distributions of fish larvae and macrozooplanktonic prey might have horizontal components. To contradict the argument that food-seeking did not bring postflexion larvae near the bottom, one would need to invoke either an afternoon increase of some two orders of magnitude in copepod abundance (Table 4) or else the presence of flexion and postflexion larvae throughout the water column in morning and midday followed by their sudden disappearance in the afternoon.

A two-order-of-magnitude change in copepod species abundance over a distance of roughly 1 km (2 hours at 14 cm s^{-1}) is certainly possible; though zooplankton structures reported from the southern California continental shelf are generally larger than this (Star and Mullin 1981; Barnett and Jahn 1987), there is always the possibility of sampling the edge of a patch. Since no such edge was evident in the abundance or overall composition of microplankton or of phytoplankton, it seems unlikely that a macrozooplankton change of this order occurred. Moreover, the main copepod eaten, *Corycaeus anglicus*, is generally more abundant in midwater than near the bottom over the shallow shelf (A. Barnett[4]), in accord with its apparent distribution in this study. As to a possible midwater abundance of postflexion white croaker larvae, no such concentration has ever been reported. In some nine vertical profiles taken in daylight over a 6-d period, Brewer and Kleppel (1986) took virtually all specimens >3.5 mm in their near-bottom sampler. White croaker appears similar to another abundant sciaenid, queenfish, in this regard (cf. Jahn and Lavenberg 1986).

[4]A. Barnett, Marine Ecological Consultants, 531 Encinitas Blvd., Encinitas, CA 92024, pers. commun. July 1987.

The only unequivocal instance in which a prey item of larval white croaker was vertically distributed similarly to the larvae was the trace of amphipods found in the guts of competent (flexion and postflexion) larvae. At the lengths of larvae sampled (<12 mm) the prey were all planktonic and nearly all about equally abundant in midwaters as near the bottom. The small numbers of amphipods eaten may indicate an incipient transition to larger, suprabenthic crustacean prey. The size gap between the large prey of these competent larvae and the smaller prey of preflexion larvae is probably an artifact of the bimodal size distribution of sampled larvae. Though all of the prey eaten by size-1 (<2.7 mm) larvae were <300 μm in length, the more varied diet of larger preflexion larvae contained some copepods as big as 500 μm. There is therefore nothing in these data to suggest that the switch from microplanktonic to macroplanktonic prey is anything but a gradual transition as the larvae grow.

Brewer and Kleppel (1986) also reported a change to copepod prey in white croaker larvae >6 mm. Our findings are further similar to those of Brewer and Kleppel in that there was no indication that food-seeking had anything to do with the descent of larval white croaker from midwaters to the near-bottom zone. The other definable dietary trend in this study (besides ontogenetic change) was the high percentage of rotifers eaten by midwater preflexion larvae. This was apparently related to subtle but important differences in the available planktonic prey—significantly, to a greater abundance of suitable-size rotifers—at the time the midwater stratum was sampled.

It seems safest to conclude that white croaker larvae descend toward the bottom for reasons quite apart from seeking food (see discussions in Barnett et al. [1984], Brewer and Kleppel [1986], Jahn and Lavenberg [1986]) and simply eat whatever they find there that suits them. Many potential macroplanktonic prey also favor the near-bottom layer (Jahn and Lavenberg 1986; Barnett and Jahn 1987). Older larvae and their prey may occupy the near-bottom layer for different reasons, or it may be that a single advantage, or set of pressures, underlies the behavior of these diverse planktonic and semi-planktonic taxa. Some species need to remain near shore, and living in the bottom boundary layer helps assure this. The boundary layer also tends to be more turbid than overlying waters and so may lessen an animal's jeopardy to visual (biting) planktivores. (The generality of the latter explanation only holds if suprabenthic fish larvae are less important planktivores than other water-column inhabitants—see Cushing 1983.)

Rotifers have never to our knowledge been reported as an important food of ocean-caught fish larvae, even though the genus *Brachionus* is commonly cultured for feeding larval fish in the laboratory. Schmitt (1986) reported that small, laboratory-reared larval northern anchovy readily fed upon (unidentified) wild-caught rotifers. Rotifers are only occasionally abundant in neritic waters, and never in oceanic waters (J. Beers[5]). Their rarity notwithstanding, rotifers have the ability very rapidly to dominate marine microplanktonic assemblages (Hernroth 1983), and their good food quality (Theilacker 1987) and high secondary productivity for a period of weeks might constitute a significant enhancement to growth and survival of a larval fish cohort.

Our previous experience in handling larval white croaker specimens agrees with the findings of Brewer and Kleppel (1986) in that lamellibranch larvae, easily seen through the body wall, are a common food for small white croaker larvae. In our study, this taxon was a minor constituent of the plankton and of the larval fish diet. We cannot say how unusual were the circumstances we encountered, but we know that in terms of diatom numbers and larval fish diversity these conditions were not typical of March on the southern California continental shelf. That white croaker larvae appeared to find these conditions salubrious may be one reason this species is so successful in southern California (Love et al. 1984).

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[5]J. Beers, Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun. November 1986.

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LITERATURE CITED

ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull., U.S. 74:517–530.

BALON, E. K.
1975. Terminology of intervals in fish development. J. Fish. Res. Board Can. 32:1633–1670.

BARNETT, A. M., AND A. E. JAHN.
1987. Pattern and persistence of a nearshore planktonic ecosystem off southern California. Cont. Shelf Res. 7:1–25.

BARNETT, A. M., A. E. JAHN, P. D. SERTIC, AND W. WATSON.
1984. Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. Fish. Bull., U.S. 82:97–111.

BREWER, G. D., AND G. S. KLEPPEL.
1986. Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California. Mar. Ecol. Prog. Ser. 27:217–226.

BREWER, G. D., G. S. KLEPPEL, AND M. DEMPSEY.
1984. Apparent predation on ichthyoplankton by zooplankton and fishes in nearshore waters on southern California. Mar. Biol. (Berl.) 80:17–28.

BREWER, G. D., R. L. LAVENBERG, AND G. E. MCGOWEN.
1981. Abundance and vertical distribution of fish eggs and larvae in the Southern California Bight: June and October 1978. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:165–167.

BUCKLEY, L. J., AND R. G. LOUGH.
1987. Recent growth, biochemical composition, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. Can. J. Fish. Aquat. Sci. 44:14–25.

CLUTTER, R. I.
1969. The microdistribution and social behavior of some pelagic mysid shrimps. J. Exp. Mar. Biol. Ecol. 3:125–155.

CUSHING, D. H.
1983. Are fish larvae too dilute to affect the density of their food organisms? J. Plankton Res. 5:847–854.

EFRON, B.
1982. The jackknife, the bootstrap and other resampling plans. Soc. Ind. Appl. Math., Philadelphia, PA, 92 p.

GADOMSKI, D. M., AND G. W. BOEHLERT.
1984. Feeding ecology of pelagic larvae of English sole, *Parophrys vetulus*, and butter sole, *Isopsetta isolepis*, off the Oregon coast. Mar. Ecol. Prog. Ser. 20:1–12.

GOVONI, J. J., D. E. HOSS, AND A. J. CHESTER.
1983. Comparative feeding of three species of larval fishes in the northern Gulf of Mexico: *Brevoortia patronus*, *Leiostomus xanthurus*, and *Micropogonias undulatus*. Mar. Ecol. Prog. Ser. 13:189–199.

GOVONI, J. J., A. J. CHESTER, D. E. HOSS, AND P. B. ORTNER.
1985. An observation of episodic feeding and growth of larval *Leiostomus xanthurus* in the northern Gulf of Mexico. J. Plankton Res. 7:137–146.

HAMNER, W. M., AND J. H. CARLETON.
1979. Copepod swarms: attributes and role in coral reef ecosystems. Limnol. Oceanogr. 24:1–14.

HERNROTH, L.
1983. Marine pelagic rotifers and tintinnids—important trophic links in the spring plankton community of the Gullmar Fjord, Sweden. J. Plankton Res. 5:835–846.

HUNTER, J. R.
1981. Feeding ecology and predation of marine fish larvae. *In* R. Lasker (editor), Marine fish larvae: morphology, ecology, and relation to fisheries, p. 34–77. Washington Sea Grant Program, Seattle.

JAHN, A. E., AND R. J. LAVENBERG.
1986. Fine-scale distribution of nearshore, suprabenthic fish larvae. Mar. Ecol. Prog. Ser. 31:223–231.

LASKER, R.
1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453–462.
1978. The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:212–330.

LAVENBERG, R. J., G. E. MCGOWEN, A. E. JAHN, J. H. PETERSEN, AND T. C. SCIARROTTA.
1986. Southern California nearshore ichthyoplankton: a study of abundance patterns. CalCOFI Rep. 27:53–64.

LEIS, J. M.
1986. Epibenthic schooling by larvae of the clupeid fish *Spratelloides gracilis*. Jpn. J. Ichthyol. 33:67–69.

LOVE, M. S., G. E. MCGOWEN, W. WESTPHAL, R. J. LAVENBERG, AND L. MARTIN.
1984. Aspects of the life history and fishery of the white croaker, *Genyonemus lineatus* (Sciaenidae), off California. Fish. Bull., U.S. 82:179–198.

MCGOWEN, G. E.
1987. Coastal zone ichthyoplankton assemblages off Southern California. Ph.D. Thesis, Univ. Southern California, Los Angeles, 304 p.

OWEN, R. W.
1981. Microscale plankton patchiness in the larval anchovy environment. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:364–368.

SAINTE-MARIE, B., AND P. BRUNEL.
1985. Suprabenthic gradients of swimming activity by cold-water gammaridean amphipod crustacea over a muddy shelf in the Gulf of Saint Lawrence. Mar. Ecol. Prog. Ser. 23:57–69.

SCHLOTTERBECK, R. E., AND D. W. CONNALLY.
1982. Vertical stratification of three nearshore southern California larval fishes (*Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*). Fish. Bull., U.S. 80:895–902.

SCHMITT, P. D.
1986. Prey size selectivity and feeding rate of larvae of the northern anchovy, *Engraulis mordax* Girard. CalCOFI Rep. 27:153–161.

STAR, J. L., AND M. M. MULLIN.
1981. Zooplanktonic assemblages in three areas of the North Pacific Ocean as revealed by continuous horizontal transects. Deep-Sea Res. 28A:1303–1322.

TANAKA, M.
1985. Factors affecting the inshore migration of pelagic larval and demersal juvenile red sea bream, *Pagrus major*, to a nursery ground. Trans. Am. Fish. Soc. 114:471–477.

THEILACKER, G.
1987. Feeding ecology and growth energetics of larval northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 85:213–228.

THEILACKER, G., AND K. DORSEY.
1980. Larval fish diversity, a summary of laboratory and field research. FAO Intergov. Oceanogr. Comm. Workshop Rep. No. 28, p. 105–142.

TONT, S. A.
1981. Historical changes of diatom abundance off southern California as reflected in sea surface temperature, air temperature, and sea level. J. Mar. Res. 39:191–201.

UTERMÖHL, N.
1931. Neue Wege in der quantitativen Erfassung des Planktons. Verh. Int. Ver. Limnol. 5:567–597.

WALKER, H. J., JR., W. WATSON, AND A. M. BARNETT.
1987. Seasonal occurrence of larval fishes in the nearshore Southern California Bight off San Onofre, California. Estuarine Coastal Shelf Sci. 25:91–109.

WATSON, W.
1982. Development of eggs and larvae of the white croaker, *Genyonemus lineatus* Ayres (Pisces:Sciaenidae), off the southern California coast. Fish. Bull., U.S. 80:403–417.

WISHNER, K. F.
1980. The biomass of the deep-sea benthopelagic plankton. Deep-Sea Res. 27:203–216.

NEW MARINE DECAPOD CRUSTACEANS FROM WATERS INFLUENCED BY HYDROTHERMAL DISCHARGE, BRINE, AND HYDROCARBON SEEPAGE

AUSTIN B. WILLIAMS[1]

ABSTRACT

Five species of decapod crustaceans new to science are described. These are caridean shrimps of the family Bresiliidae—*Alvinocaris markensis* from a Mid-Atlantic Rift Valley hydrothermal field, *A. muricola* from a cold brine seep at the foot of the West Florida Escarpment in the Gulf of Mexico, and *A. stactophila* from a hydrocarbon seep on the continental slope of the northern Gulf of Mexico, with a key to the species of *Alvinocaris*; a squat lobster of the family Galatheidae—*Munidopsis alvisca* from the Guaymas Basin and from the Juan de Fuca and Explorer ridges in the eastern Pacific; and a brachyuran crab of the family Bythograeidae—*Bythograea mesatlantica* from a Mid-Atlantic Rift Valley hydrothermal field. Species of both *Alvinocaris* and *Bythograea* are now known from the eastern Pacific and Mid-Atlantic. *Munidopsis* species are widely represented in the world oceans.

Deep ocean hydrothermally active fields and waters influenced by brine and hydrocarbon seeps continue to yield species new to science. Such environments were unknown until explored with the aid of submersible research vessels from which observations and collections could be accomplished. The species of decapod crustaceans reported here come from hydrothermal fields in the Mid-Atlantic Rift Valley, the Guaymas Basin in the Golfo de California, and Juan de Fuca and Explorer Ridges in the northeastern Pacific, a cold brine seep at the foot of the West Florida Escarpment, and a hydrocarbon seep on the continental slope of the northern Gulf of Mexico. These are scattered localities that exhibit diverse environmental conditions but that are bound together by the common thread of chemotrophic food chains (Childress et al. 1986; Brooks et al. 1987).

The material from the Mid-Atlantic Rift Valley, West Florida Escarpment, and Guaymas Basin was observed and collected by scientists working with the aid of the DSRV *Alvin* and RV *Atlantis II* based at the Woods Hole Oceanographic Institution. That from the northern Gulf of Mexico came from the Minerals Management Service Northern Gulf of Mexico Outer Continental Slope (MMS/NGOMCS) Regional Office Project, involving observation and collection of material by scientists from LGL Ecological Research Associates and Texas A&M University, with the aid of the submersible research vessel *Johnson-Sea-Link* and its support vessels. Specimens from Explorer and Juan de Fuca Ridges were collected with the aid of the Canadian DSRV *Pisces IV* and its support vessels.

All specimens studied are deposited in the Crustacean Collection of the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

CARIDEA: BRESILIIDAE

Alvinocaris Williams and Chace, 1982

Three species of bresiliid shrimps described below as new to science are placed in the heretofore monotypic genus *Alvinocaris*. Certain features of these species necessitate minor changes in the generic diagnosis by Williams and Chace (1982) as follows: Rostrum with or without ventral teeth. Telson with 2–5 pairs of principal spines on posterior margin. Strong median sternal spine between posterior pair of pereopods.

Moreover, the branchial formula seems uniformly fixed in this genus as well as in the genus *Rimicaris* Williams and Rona, 1986. The arrangement, figured in Williams and Chace (1982) and Williams and Rona (1986) may be described as follows:

Phyllobranchs extensively developed in 2 series; asymmetrically Y-branched pleurobranchs with relatively short ventral and progressively longer and more expansive dorsal ramus associ-

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ated with pereopods 1–5; smaller and more nearly symmetrical U-branched arthrobranchs of more nearly uniform size associated with third maxilliped and pereopods 1–4.

Key to Known Species of *Alvinocaris*

1. Telson with terminal margin slightly concave in midline and bearing 3–5 pairs of principal spines .... *A. lusca* Williams and Chace

   Telson with terminal margin convex and bearing only 2 pairs of principal spines ... 2

2. Rostrum with ventral margin bearing 0–1 subterminal ventral spines .... *A. stactophila* new species

   Rostrum with ventral margin bearing 4 or more subterminal ventral spines 3

3. Abdominal segment 3 with pleural margin entire .....*A. markensis* new species

   Abdominal segment 3 with pleural margin obscurely serrate .... *A. muricola* new species

Alvinocaris markensis new species

Figures 1, 2, 7

Material.—USNM 234286, Holotype ♀ (crushed), USNM 234287, Paratypes, 2 ♀ (damaged), Mid-Atlantic Rift Valley about 70 km south of Kane Fracture Zone (see Leg 106 Shipboard Scientific Party [1986]; Ocean Drilling Program Leg 106 Scientific Party [1986]), 23°22.09'N, 44°57.12'W, 3,437 m, *Alvin* Dive 1683, MARK vent, Stn. 1, scoop, 30 May 1986, pilot D. Foster, observers S. Humphris and J. Edmond. From NSF Ocean Drilling Program-Leg 106, NSF Grant OCE-8311201 to J. F. Grassle, Woods Hole Oceanographic Institution, Woods Hole, MA.

Measurements in mm.—Holotype ♀, postorbital carapace length 4.16, rostrum 2.3, maximum carapace height 3.3, total length about 15.6. Paratype ♀, same 2.7, 1.6, 2.4, 10.9.

Description.—Integument extremely thin, membranous, shining, with a few minute punctations. Rostrum (Fig. 1*a*, *b*) almost straight, slightly elevated above horizontal in distal half, sharply pointed tip usually reaching to between midlength of second and tip of third peduncular articles of antennule; dorsal margin raised into thin serrate crest containing 12–17 teeth, strongest in central sector of row, with about 1/3 length of crest continued onto carapace; ventral margin less prominent and armed with 5–8 subterminal teeth; tooth formulas examined, 17/8 (holotype), 17/5, 12/5 (apparently some subterminal dorsal teeth fused); strong lateral carina broadened proximally and confluent with orbital margin. Carapace with acute antennal spine distinct; pterygostomian spine acuminate and prominent. Indistinct antennal groove curving ventrad to intersect associated indistinct groove at about midlength of carapace and continuing posteriad.

Abdomen of female (Fig. 1*c*) apparently broadly arched dorsally (all specimens examined are crushed), gradually tapering posteriorly, narrowest part of sixth somite about 1/2 width of first somite; pleura of 3 anterior somites broadly rounded, that of fourth somite drawn posterolaterally to strong acuminate spine flanked dorsally by 0 or 1 much more slender and smaller spine; posterolateral corner of fifth pleuron strongly acuminate to nearly right angled and flanked dorsally by 0–2 spines of variable size analogous to condition on somite 4, spine number possibly age related; sixth somite with middorsal length about 1.9 that of fifth, broad based midlateral spine overlapping base of telson, smaller posterolateral spine acute; fourth somite with small erect spine on sternite and fifth with analogous strong, posteriorly directed spine. Telson (Fig. 1*d*) elongate subrectangular, length about 3.5 anterior width, 5.8 posterior width, and about 1.75 length of sixth somite, not including posterior spines; armed with 6–8 dorsolateral spines of nearly uniform size, sometimes bilaterally unequal in number; posterior margin convex, armed with 2 principal spines at each corner and 10–12 feathered strong setae on margin between.

Eyes (Fig. 1*a*, *b*) with cornea imperfectly developed, unfaceted though diffusely pigmented, globular to ovate in outline and with prominent spine on anterodorsal edge.

Antennular peduncle (Fig. 1*a*, *b*) reaching end of antennal scale; basal article 1.3 length of second and about 3.0 length of third, stylocerite well

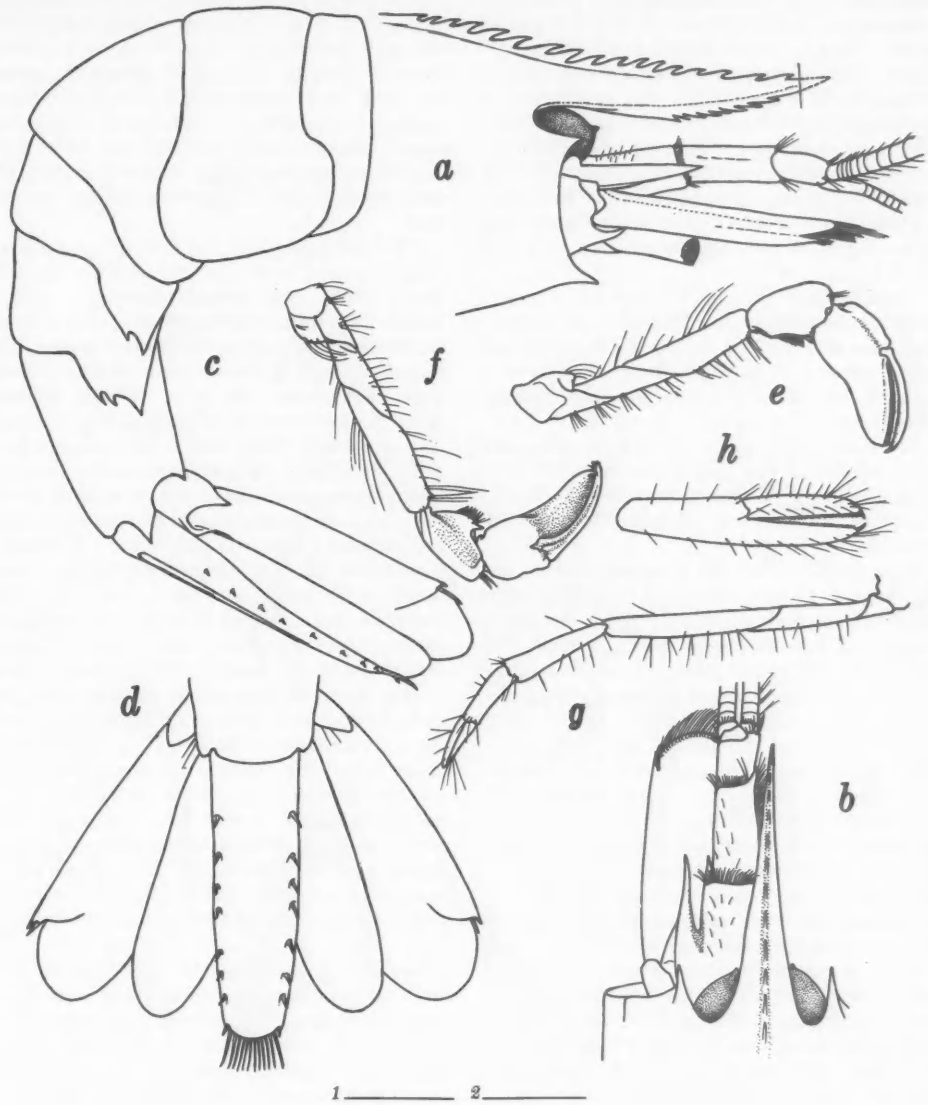

FIGURE 1.—*Alvinocaris markensis*, holotype ♀: *a* part of cephalothorax and anterior appendages, lateral; *b* rostrum, eye, antennular peduncle, antennal scale, dorsal of left side; *c* abdomen, lateral; *d* tail fan; cheliped, *e* mesial, *f* lateral; *g* pereopod 2, *h* chela. Scales = 2 mm: 1 (*a*, *c*, *d*, *e*, *f*, *g*, *h*); 2 (*b*).

separated from peduncle, tapering to slender elongate tip reaching about 1/4 length of second article, basal article with distodorsal margin flanked by transverse row of setae, extended into strong lateral spine reaching level equal to that of stylocerite and closely appressed to second article; shorter second article with strong mesiodistal appressed spine. Dorsolateral flagellum about 1.5 length of carapace, thickened proximal half bearing conspicuous ventral setae; ventromesial flagellum somewhat more slender in lateral view and shorter.

Antennal scale (Fig. 1*a*, *b*) about 2.5 as long as wide, distolateral tooth falling short of distomesial apex of broadly rounded distal margin of blade; basal article with strong ventrolateral spine; flagellum slightly exceeding length of body (missing from holotype).

Mandibles (Fig. 2*g*) similar, with 2-segmented palp, incisor process broad and armed with 8 marginal teeth, slender molar process simple, divergent, its narrowly rounded tip minutely setose.

First maxilla (Fig. 2*h*) with proximal endite asymmetrically oval-triangular, distal margin bearing many long setae; distal endite with narrowed base but broadened distally, armed with many (about 37) short spines on mesial margin and with scattered longer spinules marginally and submarginally beyond either end of spine row; palp scarcely bifurcated, with long distal spine on obsolescent proximomesial branch and 1 shorter submarginal spine on distal branch.

Second maxilla (Fig. 2*i*) with proximal endite represented by 2 similar lobes; distal endite subtriangular, expanded mesiodistally and paralleled laterally by narrow somewhat twisted palp, scaphognathite with anterior lobe rectangulo-ovate, fringed with uniformly long, silky setae on anterior and mesial borders, shorter setae along entire lateral margin; posterior lobe narrowly ovate-triangular, fringed on blunt tip and adjacent mesial margin by strikingly long, tangled, strong setae preceded proximally by shorter setae similar to those on lateral margin.

First maxilliped (Fig. 2*j*, partly flattened view) with irregularly fusiform endite, short palp much exceeded in length and size by leaflike exopod, epipod obscurely bilobed.

Second maxilliped (Fig. 2*k*, *l*) somewhat pediform but flattened, mesial margin of articles bearing long, feathered setae, mesial surface of terminal article densely setose, tip of exopod exceeding leaflike epipod.

Third maxilliped (Fig. 2*m*, *n*) slender, 5-segmented, reaching beyond antennular peduncle; terminal segment trigonal in cross section, tapered distally, bearing 3 terminal spines, oblique tracts of dense setae along mesial surface; similar tract of setae on carpus and another less conspicuous group on merus-ischium, latter with distolateral spine at articulation with carpus; exopod much reduced, ovate-triangular, without lash.

First pereopods (Fig. 1*e*, *f*) chelate, subequal; fingers curved ventrally and slightly laterad; dactyl much more slender than and slightly longer than fixed finger; mesial surface of each finger convex, lateral surface deeply concave; prehensile surfaces uniformly offset, closing without gape, each armed with row of almost uniform teeth so closely set as to be almost contiguous, line of sensory hairs mesial to cutting edges, acute tip of dactyl slightly spooned by elongate teeth slanted distad and curving around its external edge. Leg not reaching tip of third maxilliped and exceeding antennal peduncle. Palm of holotype female inflated, length slightly greater than height and shorter than fingers (0.60); low ridge ending in small hooked spine on proximomesial surface near articulation with carpus. Carpus longer than palm; bearing oblique ventral crest ending in strong distoventral spine and flanked mesially by patch of setae on triangular raised area; rectangular distal notch above spine followed by oblique distomesial margin leading to poorly defined spine at condyle articulating with palm; distolateral margin with rounded ventral corner leading to sinuous border above it bearing 2 lobes near articulation with palm. Merus somewhat swollen is distal half and bearing small distomesial spine, distinct from ischium but fused to it.

Second pereopod (Figs. 1*g*, *h*; 7*l*) shorter and more slender than first, but reaching beyond antennal peduncle by about length of fingers. Fingers slightly shorter than palm, similar in size and shape; opposed edges without gape, each spineless proximally, but distal half pectinate with single row of spines directed obliquely distad and increasing slightly in size to end in noticeably stronger spine crossing opposite member when closed. Carpus slender, about 0.9 length of chela; merus and ischium unarmed.

Third to fifth pereopods (Fig. 2*a*–*f*) similar in length and structure, third reaching distal edge of antennal scale. Length articles of these legs in holotype ♀, mm:

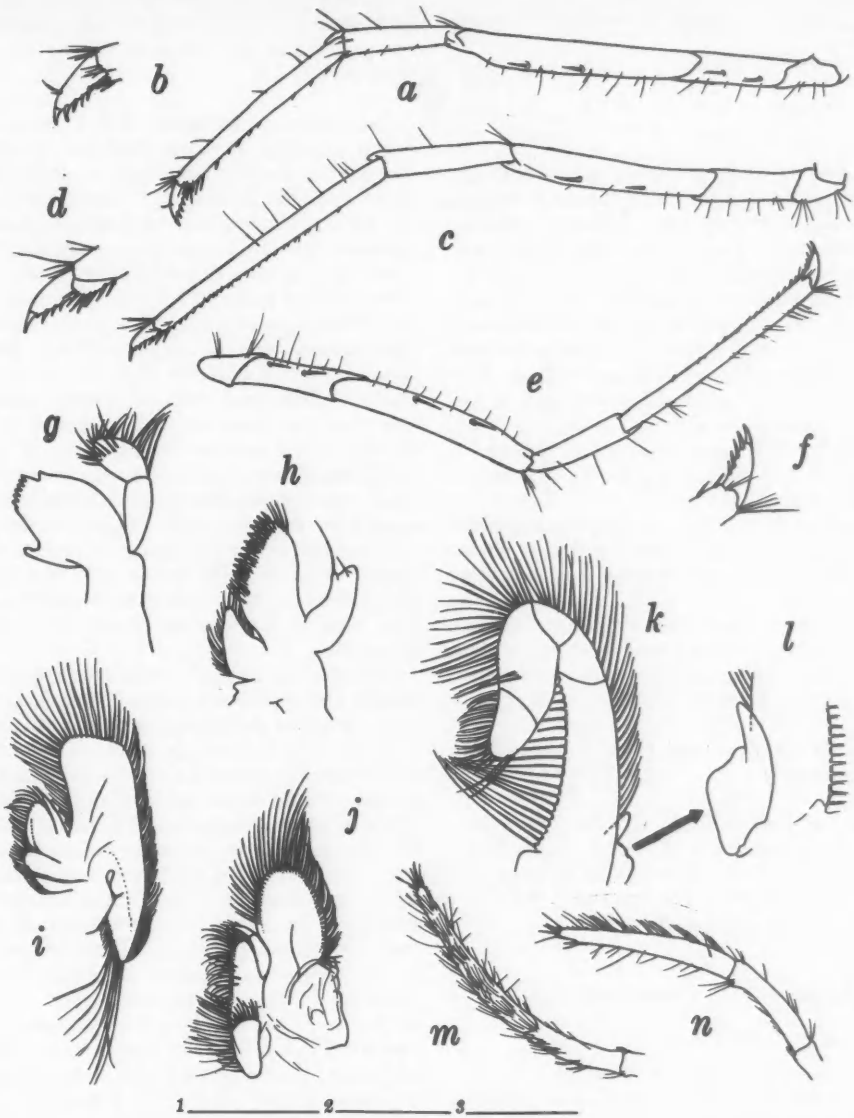

FIGURE 2.—*Alvinocaris markensis*, holotype ♀: *a* pereopod 3, *b* dactyl; *c* pereopod 4, *d* dactyl; *e* pereopod 5, *f* dactyl; *g* mandible; *h* maxilla 1; *i* maxilla 2; *j* maxilliped 1 partly flattened; maxilliped 2, *k* endopod, ventral, *l* part of exopod dorsal; maxilliped 3, *m* ventral, *n* dorsal, distal articles only. Scales: 1(*k*, *l*) = 1 mm; 2 (*b*, *d*, *f*, *g*, *h*) = 1 mm; 3 (*a*, *c*, *e*, *i*, *j*, *m*, *n*) = 2 mm.

	ischio-merus	*carpus*	*propodus*	*dactyl*
3rd	6.14	2.56	3.78	0.64
4th	5.76	2.18	4.12	0.70
5th	5.44	2.30	5.44	0.64

Each short dactyl armed with 5 spines on flexor surface, grading from small proximally to longest and strongest distally, often a sensory seta on extensor surface. Propodi with setae along flexor surface progressively more crowded distally. Carpi with distodorsal extension projecting as a stop along proximal part of propodal extensor surface. Third leg stronger, at least in merus-ischium, than fourth and fifth; merus of third and fourth with closely appressed ventral spine at 1/2 and 3/4 length, that of fifth with spines at 1/3 and 2/3 length, distal spine strongest in each case; ischium of third and fourth leg with 2 spines in line with those on merus.

Pleopods well developed, pair 1 with endopods about half length of exopods, tapering to acute tip; appendices internae simple, that of pair 5 with blunt tip.

Uropod (Fig. 1*d*) with rami subequal in length, slightly exceeding distal end of telson, lateral ramus with movable spine mesial to smaller distolateral tooth, diaeresis sinuous.

Remarks.—Remarks are given in the account for *A. stactophila*.

Etymology.—The name is taken from an acronym for the site of collection in the Mid-Atlantic Ridge Valley about 70 km south of an area known as the Kane Fracture Zone, "MARK", and the Latin genitive suffix "ensis".

Alvinocaris muricola new species

Figures 3, 4, 7

Material.—USNM 234288, Holotype ♂ (cephalothorax and abdomen broken apart), USNM 234289, Allotype ♀, West Florida Escarpment, 26°01'N, 84°54.61'W, 3,277 m, *Alvin* Dive 1754, 15 October 1986, pilot W. Sellers, observers R. Carney and B. Hecker. USNM 234290, Paratype ♀, West Florida Escarpment, same locality, *Alvin* Dive 1753, 14 October 1986, pilot P. Tibbetts, observers R. Carney and G. Knauer. All from Barbara Hecker, Lamont Geological Observatory, Columbia University, Palisades, NY.

Measurements in mm.—Holotype ♂, postorbital carapace length 6.4, rostrum 4.4, maximum carapace height 4.5. Allotype ♀, same, 6.4, rostrum broken, 5.6.

Description.—Integument thin, shining, minutely punctate. Rostrum (Fig. 3*a*, *b*) almost straight to slightly upturned in distal half, sharply pointed tip reaching to proximal part of third peduncular article of antennule; dorsal margin raised into thin serrate crest containing 17-21 teeth varying from obliquely erect in proximal part to nearly horizontal, shorter and more distant distally, about 1/3 length of crest continued onto carapace; ventral margin much less prominent and armed with row of 6 correspondingly smaller subterminal teeth, sometimes obscure; lateral carina broadened proximally and confluent with orbital margin. Carapace (Fig. 3*a*) with broad based but slender, acuminate antennal spine; pterygostomian spine correspondingly acuminate and prominent. Prominent anterior antennal carina curving posteroventrally to intersect obliquely with carina extending from pterygostomian spine at about midlength of carapace, associated groove continuing indistinctly posteriad.

Abdomen (Fig. 3*d*, *e*, *f*) of both male and female broadly arched dorsally, gradually tapering distally, narrowest part of sixth somite less than 2/3 (0.60) width of first somite; pleura of 3 anterior somites broadly rounded, margin of third slightly serrated, that of fourth somite drawn posterolaterally to strong spine flanked dorsally by 0–3 more slender and smaller spines and preceded on ventral margin by 0–2 small spines; number, position, and shape of either lateral or ventral spines may be asymmetrical; posterolateral corner of fifth pleura acuminate and flanked dorsally by 1 or 2 spines analogous to those on somite 4; sixth somite with middorsal length about 1.7 that of fifth, broad-based midlateral spine overlapping base of telson, smaller posterolateral spine acute; fourth and fifth somites each with strong, posteriorly directed spine on sternite. Telson (Fig. 3*g*) elongate subrectangular, length about 3.0 anterior width, 6.8 posterior width, and about 1.4 length of sixth somite, not including posterior spines; armed with 7 dorsolateral spines of nearly uniform size; posterior margin convex, armed with 2 principal spines at each corner and 10 or 11 feathered strong setae on distal margin between.

Eyes (Fig. 3*a*, *b*) with cornea imperfectly developed, unfaceted though diffusely pigmented,

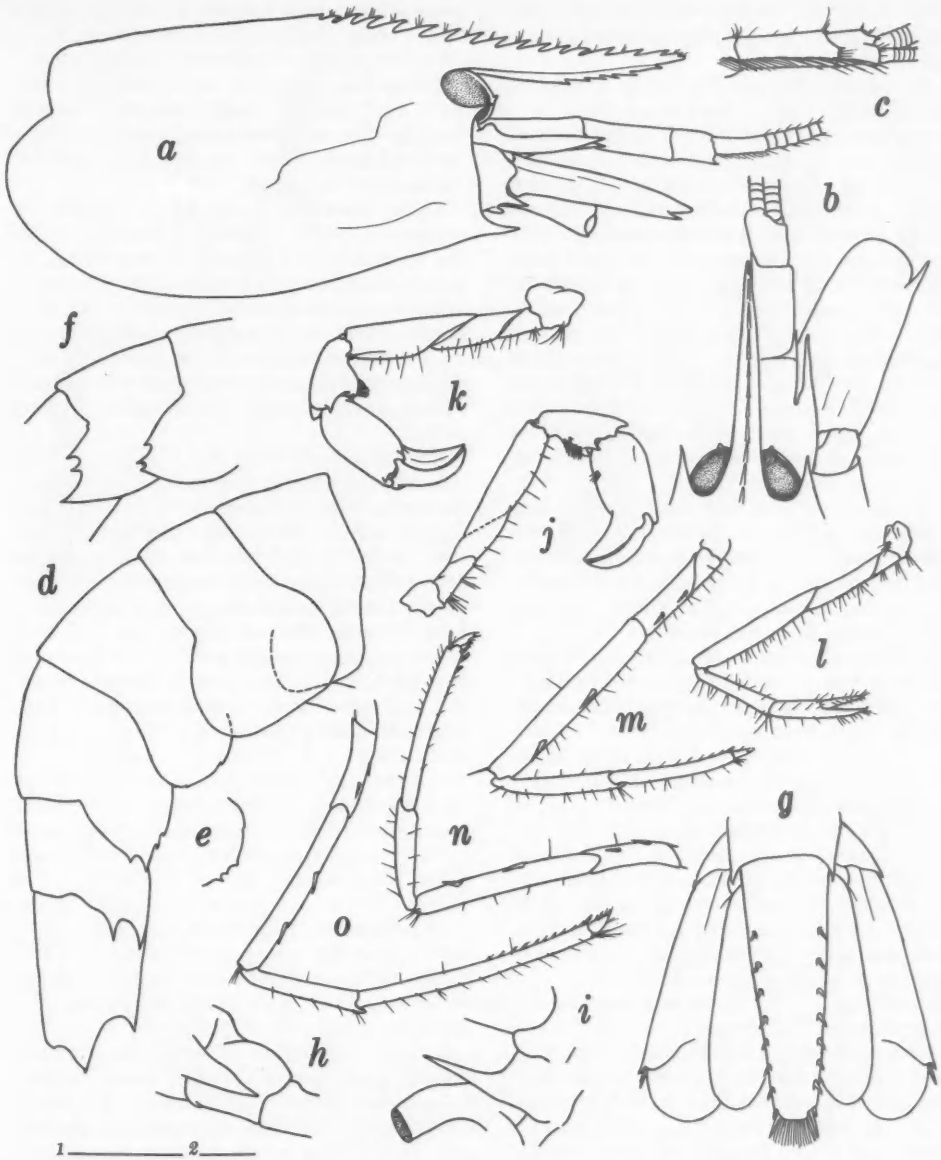

FIGURE 3.—*Alvinocaris muricola*, holotype ♂: *a* cephalothorax and anterior appendages, lateral; *b* rostrum, eye, antennular peduncle, antennal scale, dorsal of right side; *c* antennular peduncle, distal articles, mesial; abdomen with variations in spination of pleural margins (of allotype ♀), *d* lateral, *e* margin of pleuron 3 from opposite side, *f* (of holotype ♂) segments 4 and 5; *g* tail fan; *h* median sternal spine between fifth pereopods; *i* median sternal spine on abdominal segment 5; cheliped, *j* mesial, *k* lateral; *l*, *m*, *n*, *o* pereopods 2, 3, 4, 5. Scales = 1 mm: 1 (*a*–*g*, *j*–*o*); 2 (*h*, *i*).

ovate in outline, though fused to each other mesially, and each with a short upturned spine on anterior surface.

Antennular peduncle (Fig. 3*a*, *b*, *c*) reaching beyond end of antennal scale; basal article 1.1 as long as second and about 2.5 as long as third, all measured on ventral margin; stylocerite well separated from peduncle, tapering to slender elongate tip reaching tip of distolateral spine on basal article; latter exceeding distodorsal margin of article, fringed by transverse subdistal row of setae, and closely appressed to second article, distomesial spine much smaller; shorter second article with stronger mesiodistal spine. Dorsolateral flagellum about length of carapace, thickened in basal 2/3, with annulations, except at base, longer in female than in male and much longer than in whiplike distal part; ventromesial flagellum somewhat shorter and with annulations of variable but shorter length.

Antennal scale (Fig. 3*a*, *b*) about twice as long as wide, distolateral tooth strong, falling slightly short of broadly rounded distal margin of blade; basal article with acute distal spine ventrally; flagellum (broken in material studied) probably slightly exceeding length of body.

Mandibles (Fig. 4*a*) similar, with 2-segmented palp, incisor process broad and armed with 8 marginal teeth, slender molar process simple, divergent, its narrowly rounded tip minutely setose.

First maxilla (Fig. 4*b*) with proximal endite asymmetrically oval-triangular, distal margin bearing many long setae; distal endite with narrowed base but broadened distally, armed with many (about 30) short spines on mesial margin and with scattered longer spinules submarginally and marginally beyond either end of spine row; palp scarcely bifurcated, with long distal spine on obsolescent proximomesial branch and 1 shorter submarginal spine on distal branch.

Second maxilla (Fig. 4*c*, *d*) with proximal endite represented by 2 similar lobes; distal endite subtriangular, expanded mesiodistally and paralleled laterally by narrow, somewhat twisted palp; scaphognathite with anterior lobe rectangulo-ovate, fringed with uniformly long, silky setae on anterior and mesial borders, uniformly shorter setae along entire lateral margin; posterior lobe narrow and acuminate, fringed on blunt tip and adjacent mesial margin by strikingly long, strong, tangled setae preceded proximally by shorter setae similar to those on lateral margin.

First maxilliped (Fig. 4*e*, *f*) with irregularly fusiform endite, short palp concealed and much exceeded in length and size by leaflike exopod, epipod obscurely bilobed; indistinct mesial lobule on exopod possibly representing incipient lash.

Second maxilliped (Fig. 4*g*, *h*) somewhat pediform but flattened, mesial margin of articles bearing long, feathered setae, mesial surface of terminal article densely setose, exopod barely exceeding leaflike epipod.

Third maxilliped (Fig. 4*i*, *j*) slender, 5-segmented, reaching beyond antennular peduncle; terminal article trigonal in cross section, tapered distally, bearing 3 spines, transverse tracts of dense setae along mesial surface; similar tract of setae on carpus and another conspicuous group mesiodistally on merus-ischium, latter with stout distolateral spine at articulation with carpus; exopod much reduced, subtriangular, without lash.

First pereopods (Figs. 3*j*, *k*; 7*f*–*k*) chelate, subequal and sexually dimorphic, at least in fully mature individuals; fingers curved ventrally and slightly laterad; dactyl more slender than and with level of tip slightly shorter than or equal to that of fixed finger; mesial surface of each finger convex, lateral surface concave, with opposed surfaces uniformly offset; closing without gape, each armed on prehensile edge with row of almost uniform teeth so closely set as to be almost contiguous, acute tip of dactyl slightly spooned by elongate teeth slanted distad and curving around its external edge; line of sensory hairs mesial to cutting edges. Leg shorter than to almost equaling third maxilliped. Palm of holotype male inflated laterally, but apparently somewhat irregularly concave mesially, length 1.4 greatest height and longer than fingers; palm relatively shorter in allotype female, 0.3 length of fingers. Carpus shorter than palm, with oblique ventral crest ending in strong distolateral spine, flanked mesially by patch of setae on polygonal raised area. Merus somewhat swollen in distal half, distinct from ischium but fused to it, neither armed.

Second pereopod (Figs. 3*l*; 7*e*) shorter and more slender than first, reaching about to end of antennal peduncle; fingers slightly longer than palm, similar in size and shape, opposed edges without gape, each pectinate with single row of teeth in distal half directed obliquely distad and increasing slightly in size to end in noticeably stronger tooth crossing opposite member when closed, but spineless proximally; carpus slender, about 1.16 longer than chela; merus and ischium unarmed.

Third to fifth pereopods (Fig. 3*m*, *n*, *o*) similar in length and structure, third reaching to tip of or

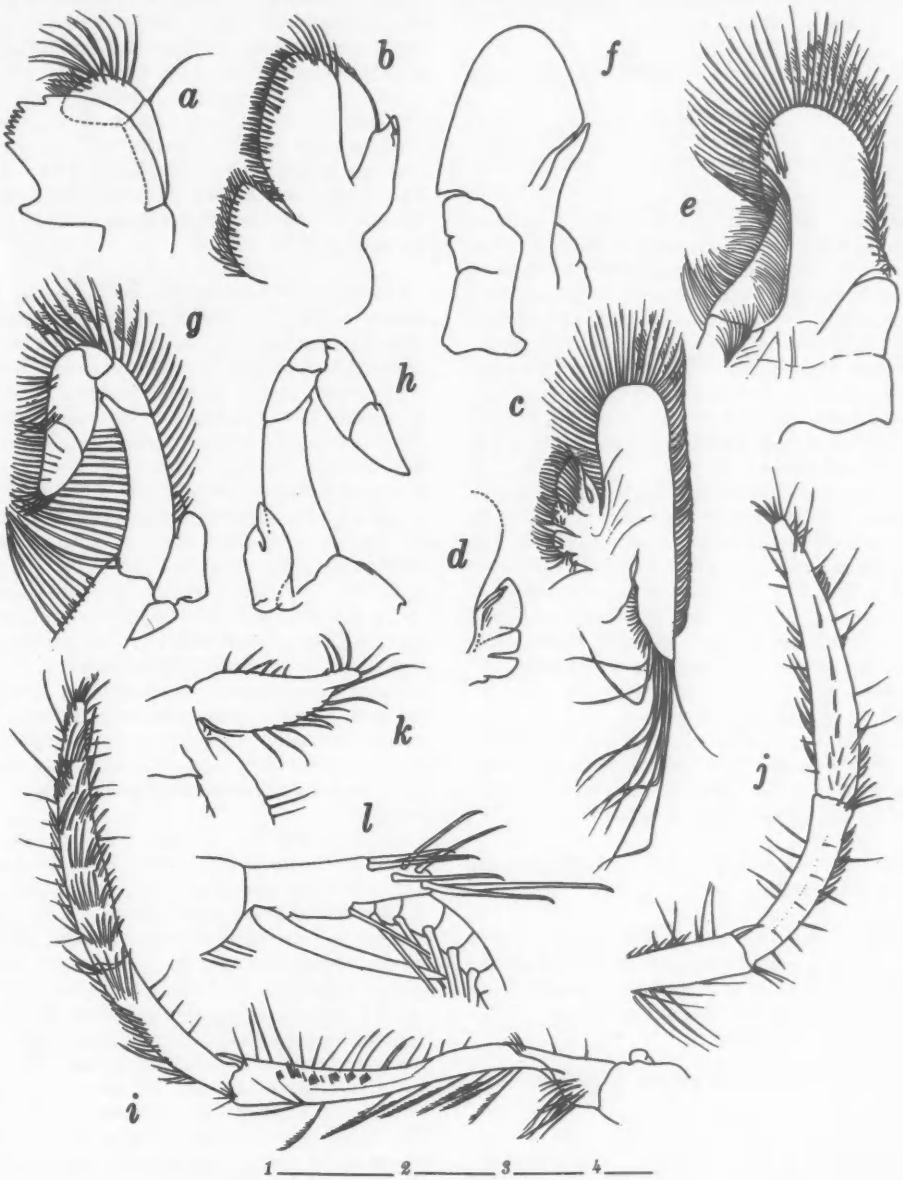

FIGURE 4.—*Alvinocaris muricola*, holotype ♂: *a* mandible; *b* maxilla 1; maxilla 2, *c* ventral, *d* palp dorsal; maxilliped 1, *e* ventral, *f* dorsal; maxilliped 2, *g* ventral, *h* dorsal; maxilliped 3, *i* ventral, *j* dorsal; *k* endopod of pleopod 1; *l* appendix masculina, pleopod 2. Scales: 1 (*e*, *f*, *g*, *j*, *o*, *k*, *l*) = 1 mm; 2 (*c*, *d*) = 1 mm; 3 (*l*) = 0.2 mm; 4 (*a*, *b*) = 0.2 mm.

slightly beyond antennal scale. Length articles of these legs in holotype ♂, mm:

	ischium	*merus*	*carpus*	*propodus*	*dactyl*
3rd	1.76	3.84	2.33	2.34	0.35
4th	1.60	3.52	1.98	3.04	0.06
5th	1.60	3.20	2.43	4.96	0.42

Each short dactyl armed with about 4–6 corneous spines on flexor surface, grading from small proximally to longest and strongest distally; carpus of each with distodorsal extension projecting as a stop along proximal part of propodal extensor surface; third leg stronger, at least in merus-ischium, than fourth and fifth, but propodus successively longer from third to fifth; merus of each with ventral spine at 1/3 and 2/3 length; ischium of third, fourth, and fifth leg with 2 spines in line with those on merus.

Pleopods well developed; first pair with endopods about 1/2 length of exopods in both sexes, narrowed into distomesial projection in male (Fig. 4*k*) but evenly tapered in female; appendix masculina (Fig. 4*l*) of second pair in male (holotype) armed with 7 slender spines extending beyond level of simple slender appendix interna; endopods of third to fifth in male and second to fifth in female with simple slender appendix interna, but that of fifth blunt tipped.

Uropod (Fig. 3*g*) with rami subequal in length, lateral ramus slightly exceeding distal end of telson, and with movable spine mesial to smaller distolateral tooth, diaeresis sinuous.

Remarks.—Remarks are given in the account for *A. stactophila*.

Etymology.—The name is from the Latin "muria", brine, and "cola", inhabiting, for association of the species with cold brine seeping from the base of the West Florida Escarpment.

Alvinocaris stactophila new species

Figures 5, 6, 7

Material.—USNM 234291, Holotype ♂, USNM 234292, Allotype ♀, USNM 234293, Paratypes, 5 ♂, 2 ♀; north central Gulf of Mexico about 129 km (80 miles) S of Louisiana, 27°46.94′N, 91°30.34′W, 534 m, *Johnson-Sea-Link* Dive 1879, 28 September 1986, Bush Hill hydrocarbon seep. From Linda H. Pequegnat and Randall Howard, LGL Ecological Research Associates, Bryan, TX, supported by partial funding for Minerals Management Service-Northern Gulf of Mexico contract 14-12-0001-30212.

Measurements in mm.—Holotype ♂, postorbital carapace length 7.0, rostrum 2.7, maximum carapace height 5.3, total length about 25. Allotype ♀, same 6.8, 2.0, 5.9, 24. Paratype ♂, same 4.2, 1.9, 3.2, total length not measured; paratype ♀, same, 4.9, 2.0, 4.1.

Description.—Integument thin, shining, minutely punctate. Rostrum (Fig. 5*a*, *b*) almost straight, imperceptibly elevated above horizontal in distal half, sharply pointed tip usually reaching proximal level of second peduncular article of antennule, but sometimes to proximal part of third peduncular article; dorsal margin raised into thin serrate crest containing 12–17 teeth, strongest in central sector of row, with about 1/2 length of crest continued onto carapace; ventral margin less prominent and armed with 0 or 1 subterminal tooth; sample tooth formulas 11/1, 12/0, 14/1, 17/1; lateral carina broadened proximally and confluent with orbital margin. Carapace (Fig. 5*a*, *b*) with buttressed acuminate antennal spine distinct; pterygostomian spine acuminate and prominent. Prominent anterior antennal carina curving posteroventrally to intersect obliquely with carina extending from pterygostomial spine at about midlength of carapace, associated groove continuing indistinctly posteriad.

Abdomen (Fig. 5*d*) of both male and female broadly arched dorsally, gradually tapering distally, narrowest part of sixth somite less than 1/2 (0.44) width of first somite; pleura of 3 anterior somites broadly rounded, that of fourth somite drawn posterolaterally to acuminate spine flanked dorsally by 0–3 much more slender and smaller spines; posterolateral corner of fifth pleuron varying from strongly acuminate to nearly rectangular and flanked dorsally by 2–5 spines analogous to those on somite 4; sixth somite with middorsal length about 1.8 that of fifth, broad-based midlateral spine overlapping base of telson, smaller posterolateral spine acute; fourth and fifth somites each with strong, posteriorly directed spine on sternite. Telson (Fig. 5*e*) elongate subrectangular, length about 2.8 anterior width, 5.2 posterior width, and about 1.7 length of sixth somite, not including posterior spines; armed with 5–8 dorsolateral spines of

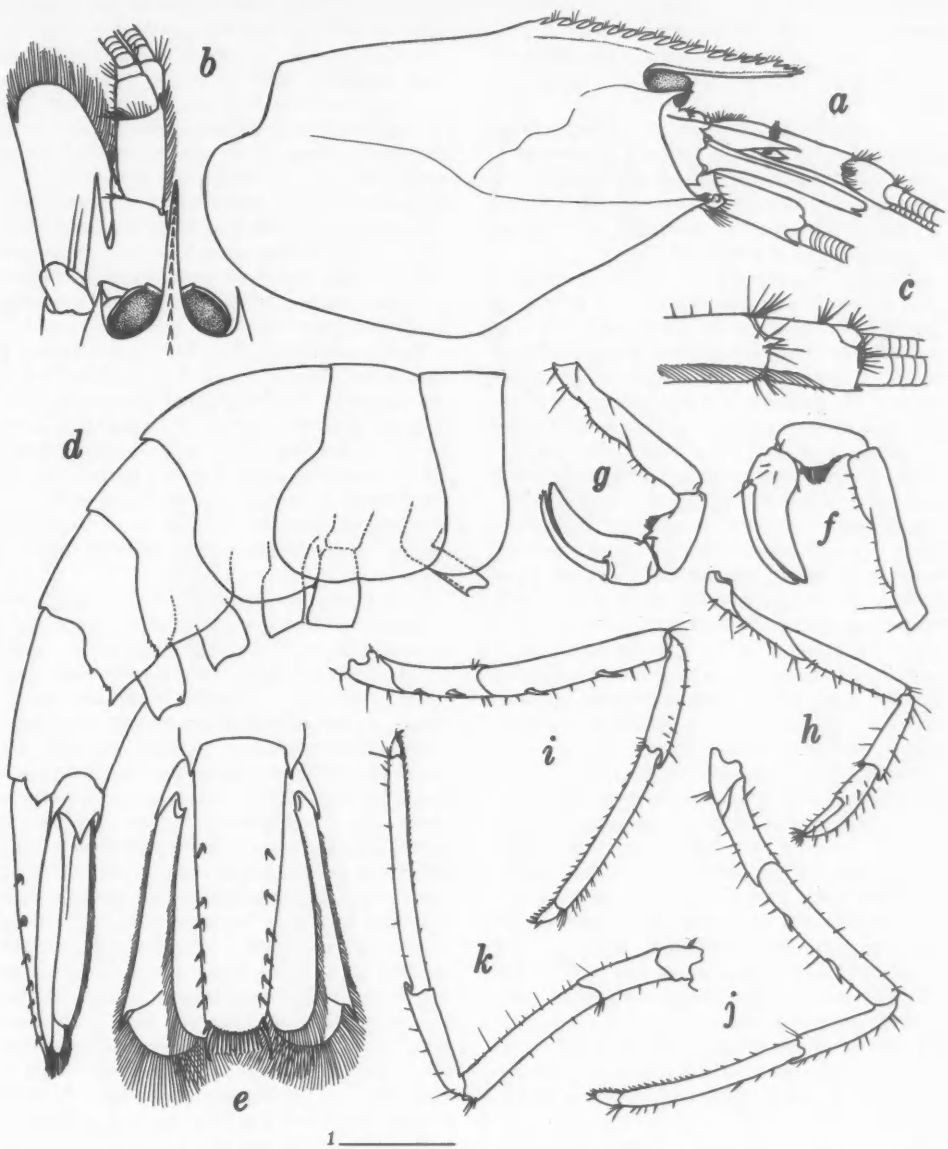

FIGURE 5—*Alvinocaris stactophila*, holotype ♂: *a* cephalothorax and anterior appendages, lateral; *b* rostrum, eye, antennular peduncle, antennal scale, dorsal of left side; *c* antennular peduncle, distal articles, mesial; *d* abdomen, lateral; *e* tail fan. Allotype ♀: cheliped, *f* mesial, *g* lateral; *h*, *i*, *j*, *k* pereopods 2, 3, 4, 5. Scale = 2 mm.

nearly uniform size, occasionally unequal in number on either side; posterior margin convex, armed with 2 principal spines at each corner and 8–12 feathered strong setae on distal margin between.

Eyes (Fig. 5*a*, *b*) with cornea imperfectly developed; unfaceted though diffusely pigmented in adults, but with internal facetlike pattern in smaller individuals; ovate in outline though fused to each other mesially, and each with an upturned spine on anterodorsal surface.

Antennular peduncle (Fig. 5*a*, *b*, *c*) reaching beyond end of antennal scale; basal article 1.3 length of second and about 2.2 length of third, all measured on dorsal margin; stylocerite well separated from peduncle, tapering to slender elongate tip variably reaching as far as midlength of second article; basal article with distodorsal margin exceeded by rostral tip though extended into strong lateral spine reaching level equal to that of stylocerite and closely appressed to second article, much smaller distomesial spine slightly divergent; shorter second article with stronger mesiodistal spine. Dorsolateral flagellum about twice length of carapace, thickened in basal half; ventromesial flagellum somewhat shorter.

Antennal scale (Fig. 5*a*, *b*) about twice as long as wide, distolateral tooth strong, falling short of broadly rounded distal margin of blade; basal article with small distal spine ventrally; flagellum slightly exceeding length of body.

Mandibles (Fig. 6*a*) similar, with 2-segmented palp, incisor process broad and armed with 7 marginal teeth, slender molar process simple, divergent, its narrowly rounded tip minutely setose.

First maxilla (Fig. 6*b*) with proximal endite asymmetrically oval-triangular, distal margin bearing about 25 long setae; distal endite with narrowed base but broadened distally, armed with many short spines on mesial margin and with scattered longer spinules submarginally and marginally beyond either end of spine row; palp scarcely bifurcated, with long distal spine on obsolescent proximomesial branch and shorter adjacent submarginal spine and tangled setae on distal branch.

Second maxilla (Fig. 6*c*) with proximal endite represented by 2 similar lobes; distal endite subtriangular, expanded mesiodistally and paralleled laterally by narrow somewhat twisted palp; scaphognathite with anterior lobe rectangulo-ovate, fringed with uniformly long, silky setae on anterior and mesial borders, uniformly shorter setae along entire lateral margin, posterior lobe narrow and acuminate, fringed on blunt tip and adjacent mesial margin by strikingly long, tangled strong setae preceded proximally by shorter setae similar to those on lateral margin.

First maxilliped (Fig. 6*d*, *e*) with irregularly fusiform endite, short palp concealed and much exceeded in length and size by leaflike exopod, epipod obscurely bilobed; indistinct mesial lobule on exopod possibly representing incipient lash.

Second maxilliped (Fig. 6*f*, *g*) somewhat pediform but flattened, mesial margin of articles bearing long, feathered setae, mesial surface of terminal article densely setose, exopod barely exceeding leaflike epipod.

Third maxilliped (Fig. 6*h*, *i*, *j*) slender, 5-segmented, reaching beyond antennular peduncle; terminal article trigonal in cross section, tapered distally, bearing 3 spines, transverse tracts of dense setae along mesial surface; similar tract of setae on carpus and another less conspicuous group on merus-ischium, latter with stout distolateral spine at articulation with carpus; exopod much reduced, subtriangular, without lash.

First pereopods (Figs. 5*f*, *g*; 7*c*, *d*) chelate, subequal and sexually dimorphic, at least in fully mature individuals; fingers curved ventrally and slightly laterad; dactyl more slender than fixed finger, tips varying slightly in relative length; mesial surface of each finger convex, lateral surface concave; prehensile surfaces uniformly offset, closing without gape, each armed with row of almost uniform teeth so closely set as to be almost contiguous, line of sensory hairs mesial to cutting edges, acute tip of dactyl slightly spooned by elongate teeth slanted distad and curving around external edge. Leg exceeding third maxilliped by length of fingers in holotype male, but shorter than third maxilliped in other individuals. Palm inflated in holotype male, length 1.4 greatest height and longer than fingers; palm relatively shorter in allotype female and other individuals examined, 0.3 length of fingers. Carpus shorter than palm in holotype but longer than palm in remainder of specimens examined, bearing oblique ventral crest ending in strong distolateral spine and flanked mesially by patch of setae on polygonal raised area; notch above spine smoothly concave and opposing low ridge ending in small rounded spine on heel of palm; shallowly concave anteromesial margin of carpus leading dorsally to 2 low rounded lobes. Merus somewhat swollen in distal half, distinct from ischium but fused to it, neither armed.

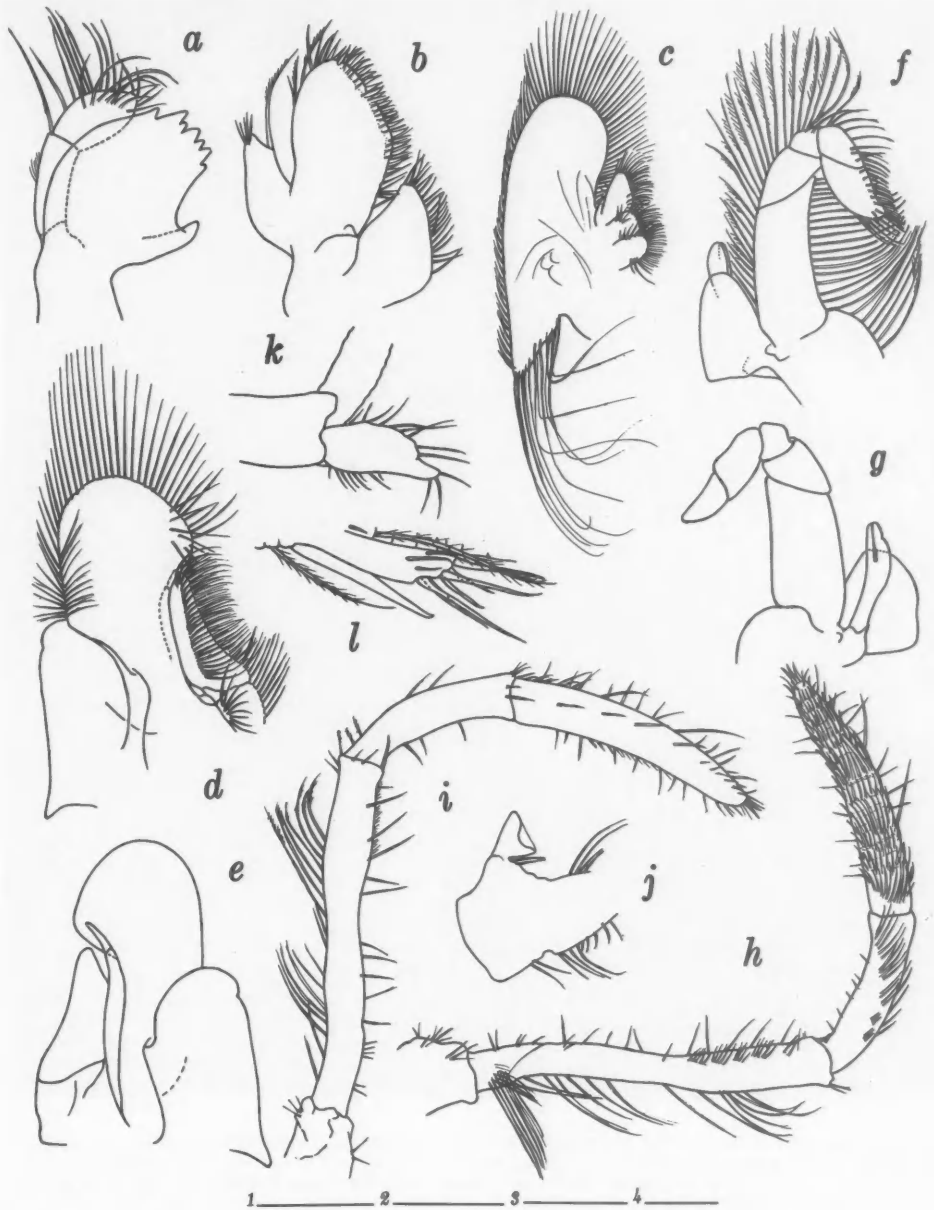

FIGURE 6.—*Alvinocaris stactophila*, allotype ♀: *a* mandible; *b* maxilla 1; *c* maxilla 2; maxilliped 1, *d* ventral, *e* dorsal; maxilliped 2, *f* ventral, *g* dorsal; maxilliped 3, *h* ventral, *i* dorsal, *j* exopod. Paratype ♂: *k* endopod of pleopod 1; *l* appendix masculina, pleopod 2. Scales: 1 (*d–g*, *k*) = 1 mm; 2 (*a*, *b*) = 0.5 mm; 3 (*l*) = 0.3 mm; 4 (*c*) = 1 mm.

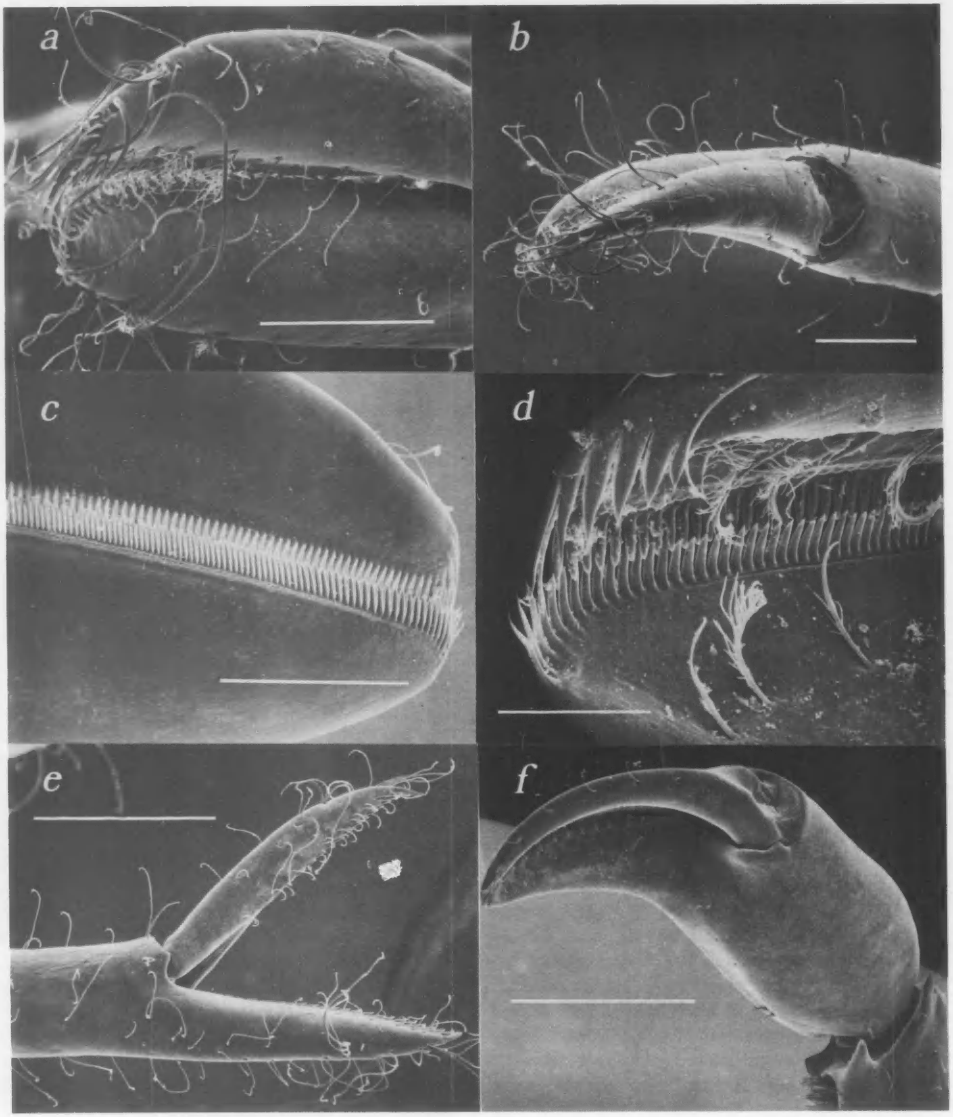

FIGURE 7.—Parts of *Alvinocaris* chelae viewed by SEM. *A. stactophila*: fingers of small chela, *a* mesial, *b* dorsal; fingers of large chela showing finely toothed opposed edges near tips, *c* mesial, teeth flush with convex surface, *d* lateral, teeth marginal on spooned tips, with points rounded on dactyl, acute on fixed finger. *A. muricola*: *e* fingers of small chela, lateral; *f* large chela and distal part of carpus, lateral. Scales: 100 μm, *d*; 200 μm, *a–c*; 500 μm, *e*; 1 mm, *f*.

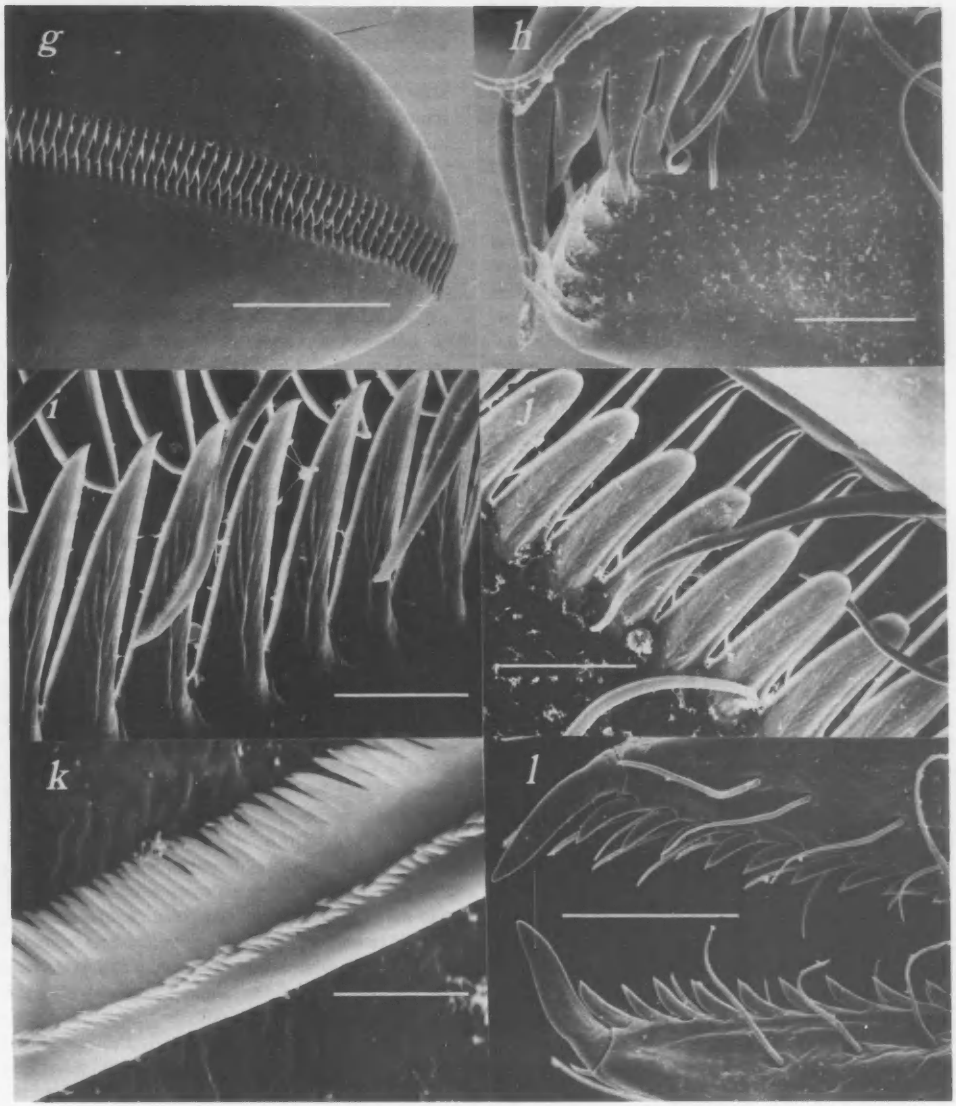

FIGURE 7.—*Continued.*—*Alvinocaris muricola*: fingers of large chela showing finely toothed opposed edges near tips, *g* teeth flush with convex mesial surface, *h* spooned lateral surface of same, points rounded on dactyl, acute on fixed finger; close-up lateral view of teeth and associated sensory setae, teeth of fixed finger in foreground and of dactyl in background, *i* near distal end of fingers, *j* near midlength of fingers; *k* sensory seta showing 2 rows of sensillae on concave surface. *A. markensis*: *l* fingers of small chela, mesial view of distal part. Scales: 3 μm, *k*; 20 μm, *i*; 30 μm, *j*; 50 μm, *h*; 100 μm, *l*; 200 μm, *g*.

Second pereopod (Figs. 5*h*; 7*a*, *b*) shorter and more slender than first, reaching to between midlength and end of antennal peduncle; fingers slightly longer than palm, similar in size and shape, opposed edges without gape, each pectinate with single row of teeth in distal half directed obliquely distad and increasing slightly in size to end in noticeably stronger tooth crossing opposite member when closed, but spineless proximally; carpus slender, about 1.2 longer than chela; merus and ischium unarmed.

Third to fifth pereopods (Fig. 5*i*, *j*, *k*) similar in length and structure, third reaching beyond antennal scale by about 0.3 length of propodus. Length articles of these legs in allotype ♀, mm:

	ischio-merus	*carpus*	*propodus*	*dactyl*
3rd	4.48	2.30	3.20	0.48
4th	4.89	2.18	3.39	0.48
5th	4.16	2.24	4.22	0.48

Each short dactyl armed with about 6 corneous spines on flexor surface, grading from small proximally to longest and strongest distally; carpus of each with distodorsal extension projecting as a stop along proximal part of propodal extensor surface; third leg stronger, at least in merus-ischium, than fourth and fifth; merus of third and fourth with ventral spine at 1/3 and 2/3 length, distal one strongest, fifth without spines; ischium of third with 2 spines in line with those on merus, that of fourth and fifth spineless.

Pleopods well developed, pair 1 with endopods about half length of expods in both sexes, endopod of male (Fig. 6*j*) with asymmetrical mesial extension, that of female tapering to acute tip; pair 2 with appendix masculina of male (Fig. 6*k*) bearing distal cluster of about 9 strong straight spinules extending beyond level of simple slender appendix interna.

Uropod (Fig. 5*e*) with rami subequal in length, slightly exceeding distal end of telson, lateral ramus with movable spine mesial to smaller distolateral tooth, diaeresis sinuous.

Etymology.—The name is from the Greek "stactos", oozing out or trickling, and "philos", to love, for association of the species with hydrocarbons seeping from the substrate.

Remarks.—*Alvinocaris lusca* and the three new species of *Alvinocaris* described here exhibit minor differences that are highlighted in the key to species given above, but their similarities seem far more significant; i.e., general body appearance and strength of integument, shape of rostrum (although that of *A. stactophila* sometimes lacks ventral teeth), shape and general armature of tail fan, blindness, and general structure of appendages, including mouthparts. Some minor differences that may be mentioned are features such as number of incisor teeth on the mandible, number of spines on the first maxilla, shape of the second maxilla, lack of meral spines on pereopod 5 in *A. stactophila*, unequal distribution of spines on ischia of pereopods 3–5 in the three species, and shape of the endopod of male pleopod 1 and appendix masculina (though males of *A. markensis* are not yet known).

Each of these species lives in a distinctive benthic environment, but all share similarities that suggest dependence on a chemotrophic bacteria-based food chain (Childress et al. 1986). Van Dover et al. (in press) provide evidence from morphology, behavioral and gut content analyses of the similar *Rimicaris exoculata* Williams and Rona that indicates a bacterial diet grazed from surfaces of hydrothermal chimneys, although direct observations of bacteria within the digestive tract could not confirm this. The distinctively spoon-shaped chelae of the first pereopods of both *Alvinocaris* and *Rimicaris* species, with unbroken comb of exceedingly fine teeth on the prehensile edges, could be an adaptation for scooping or sweeping bacteria toward the mouthparts. Williams and Chace (1982) described the first chelae of *A. lusca* as convex on the extensor surface and concave on the flexor surface, but they also said (p. 142) that the outer surface of the fingers is convex and the inner surface concave. The latter is misleading because in full extension the convex side of the chela is mesial and the concave side lateral. It is not yet known how these appendages are used, but certainly the chelae can be folded compactly against the leg's proximal articles, and in the related *Rimicaris exoculata* and *R. chacei* (Williams and Rona 1986) these legs seem very mobile. Sensillae flanking prehensile surfaces of the fingers seem well adapted to aid feeding on finely particulate matter. Moreover, the species of *Rimicaris* have exceedingly setose mouthparts.

In species of both genera, the second pair of pereopods have much smaller chelae with fingers bearing long sensory setae and spines on the prehensile edges that are seemingly adapted for

grasping. For mobile animals of this morphological makeup, the most likely feeding methods in the stated environments would seem to be bacterial concentration, along with secondary predation and scavenging.

ANOMURA: GALATHEIDAE

Munidopsis alvisca new species

Figure 8

Material.—USNM 234294, ♀ Holotype, USNM 234301, ♀ Paratype, Guaymas Basin, Golfo de California, 27°00′N, 111°25′W, 2,008 m, *Alvin* Dive 1616, 8 August 1985, pilots J. Hardiman and R. Wilkes, observer J. F. Grassle. From J. F. Grassle, Woods Hole Oceanographic Institution, Woods Hole, MA.

USNM 234295, ♂ Paratype, Explorer Ridge, Magic Mountain, 49°45.6′N, 130°16.16′W, 1,818 m, *Pisces IV* Dive P-1494, Coll. No. 1877, Gulati Gusher-base, 1 July 1984, pilots-observers, Witcombe, Johnson, Tunnicliffe. USNM 234296, ♀ ovig. Paratype, Explorer Ridge, Upper Magic Mountain, 49°45.5′N, 130°16.1′W, 1,812 m, *Pisces IV* Dive P-1497, Coll. No. 1873, Lunch Hour Vent, 4 July 1984, pilots-observers, Shepherd, Juniper, Johnson. USNM 234297, ♀ ovig. Paratype, same, Coll. No. 1875, Crab Vent. USNM 234298, ♀ ovig. Paratype, same, Coll. No. 1875. USNM 234299, 2 ♀ ovig. Paratypes, Juan de Fuca Ridge, Limbo Vent (= 3 m from Holland's Hillock Axial Seamount), 45°55′N, 130°03′W, 1,545 m, *Pisces IV* Dive P-1732, Coll. No. 1934, 2 August 1986, pilots-observers, K. Shepherd, R. Embley, J. Franklin. From Verena Tunnicliffe, Biology Department, University of Victoria, B.C., Canada.

Measurements in mm.—Holotype ♀, carapace length including rostrum 23.7, margin of orbit to posterior edge of carapace 18.6, maximum carapace width 15.7; Paratype ♀ 234301, same, 27.9, 20.8, 17.3; Paratype ♂ 234295, same, 13.8, 10.2, 8.4.

Description.—Carapace (Fig. 8*a*, *c*) exclusive of rostrum distinctly longer than broad, moderately arched transversely; anterior and posterior cervical grooves apparent, depression in anterior part of cardiac region; short moderately developed rugosities on each anterior branchial region, but more distinct and transversely developed rugae on each posterior branchial region, with tendency to being continuous across anterior and central part of cardiac region; posterior margin with median concavity. Rostrum narrowly triangular, concave dorsal surface smoothly curving to upturned tip exceeding eyestalks by more than twice their length, distinct carina bearing almost imperceptible scalelike rugae diminishing to obsolescence on gastric region. Frontal margin with broad angle lateral to eyestalk followed by concave raised and sparsely ornamented margin ending in antennal spine followed in turn by almost rectangular but acute anterolateral angle. Lateral plate obliquely rugose, projecting anteriorly below antennal peduncle, its rather angular tip minutely but bluntly bispinose.

Abdomen (Fig. 8*b*) unarmed; transverse ridge of segments 2 and 3 smooth, that of segment 4 obsolescent; segments 5 and 6 smooth.

Eyes (Fig. 8*a*, *c*) moderate in size; well exposed, smoothly ovate cornea cupped within broad based movable ocular peduncle extended into elongate mesiodorsal spine, directed obliquely upward at low angle and ornamented with tiny irregular obsolescent spinules, and much shorter mesioventral spine.

Basal article of antennular peduncle with distal margin irregularly crenulate, slender dorsolateral spine and broader lateral spine flanked by cluster of irregular small spinules, an obsolescent mesiodorsal spine present. Antennal peduncle with fixed basal article extended into stout, flat ventral spine and shorter crenulate lateral spine; succeeding articles short, second bearing stout lateral angle, third unarmed, fourth with scalloped distal margin, its dorsomesial projection spinelike.

Third maxilliped (Fig. 8*e*) with ischium shorter than merus, bearing mesial crest armed with finely uniform, evenly spaced corneous teeth. Basis with 2 low spines in line with crest on ischium. Merus with obsolescent spine at posteromesial corner, mesial margin usually with another at level of propodo-carpal joint, followed after an interval by an obscure tubercle, and then by a more prominent spine at base of convex distal margin; stronger spine at anterolateral corner; lateral margin broadly arched. Carpus, propodus, and dactyl folded on merus-ischium and about as long as those two articles together, dense setation on dorsal surface of each, and distally on prehensile surface of propodus and dactyl. Sternite (Fig. 8*d*) at base of third maxil-

liped with convex crenulate anterior margin on mesial lobe, lateral lobe angular.

Epipods absent from pereopods.

Chelipeds (Fig. 8*f*) subequal, ornamented with variably ciliate rugosities tending to arrangement in longitudinal tracts; ischium with mesial ridge bearing subterminal spine and obsolescent irregular subsidiary spines; merus rough, bearing 3 mesial spines, 1 distodorsal spine, and a smaller distoventral spine; carpus with 2 spines in dorsolateral row paralleled by less prominent ventrolateral row; palm with spines on prominent

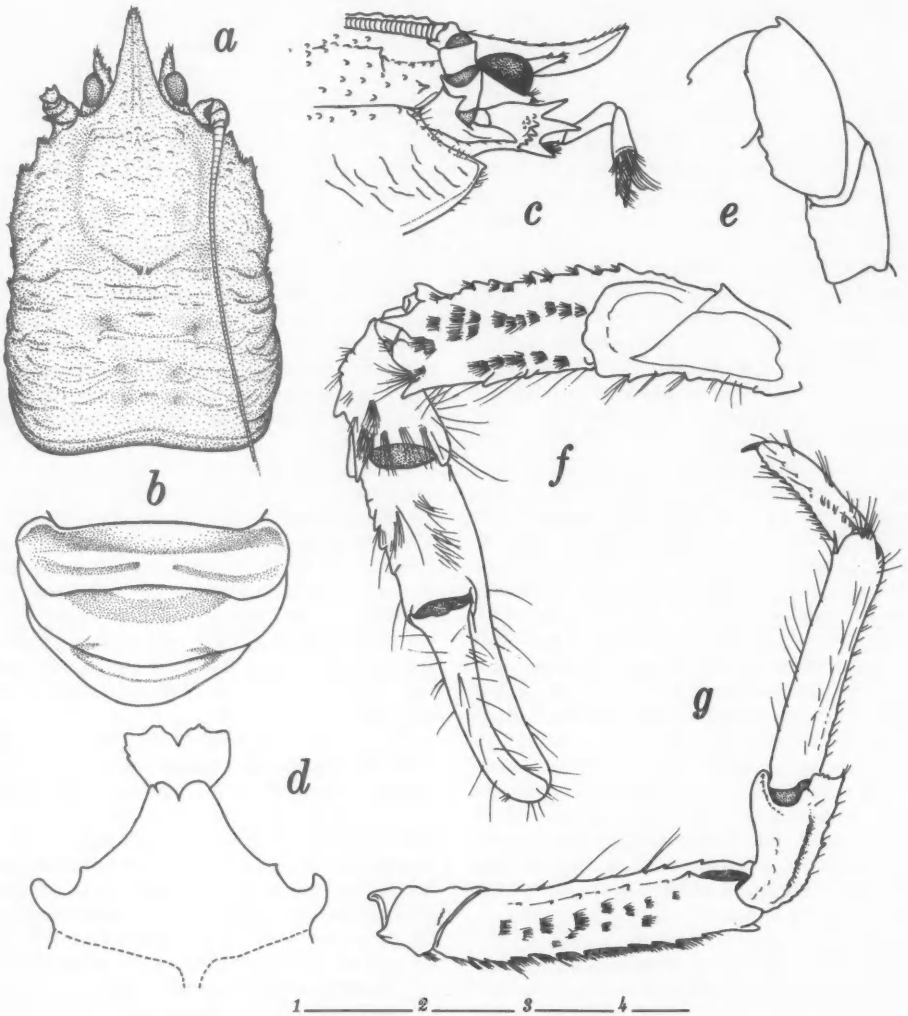

FIGURE 8.—*Munidopsis alvisca*, holotype ♀: *a* carapace, eyes and right antenna, dorsal; *b* abdomen, somites 2–4 in folded position; *c* part of cephalothorax and anterior appendages, lateral; *d* sternites at base of third maxilliped and chelipeds; *e* left third maxilliped, merus and ischium; *g* left second pereopod. Paratype ♀ 234301: *f* right cheliped. Scales: 1 (*a*, *b*) = 5 mm; 2 (*c*) = 5 mm; 3 (*f*, *g*) = 3 mm; 4 (*d*, *e*) = 1 mm.

dorsal ridge, stronger on right than on left; fingers longer than palm, spooned at tips, prehensile edges close fitting, entire, but small basal tooth of fixed finger opposed by notch in prehensile edge of dactyl.

Walking legs rather long, first walking leg (Fig. 8*g*) reaching almost to tip of chela, second and third reaching about to base of dactyl on preceding leg; corresponding articles of respective legs approximately equal in length except for meri which decrease posteriorly; each merus with rounded, rugose dorsal crest ending in distal spine; each carpus with longitudinal dorsal and dorsolateral rib ending in more or less well-developed spine, and often with secondary spine(s) on distal margin between them; each propodus slender, bearing small movable spine distolaterally at base of dactyl; each dactyl slender, acute corneous tip preceded by row of 12 or more movable spines on prehensile edge. Slender fifth leg with well-developed cleaning brush on more or less flattened dactyl opposed by similar setae on distal end of propodus.

Variation.—There is minor variation in ornamentation of the specimens available for study, but none of it is associated with the disjunct distribution in the Golfo de California and the northeastern Pacific.

Remarks.—The specimens reported here were taken around hydrothermal vent sites discussed by Canadian American Seamount Expedition (1985), ASHES Expedition (1986), and Tunnicliffe et al. (1985, 1986). *Munidopsis* has been sighted at three other sites along Juan de Fuca Ridge, but the only specimens collected are those listed above (V. Tunnicliffe[2]).

Comparisons of *Munidopsis alvisca* with previously described species of the genus are aided by reference to A. Milne Edwards (1880), Milne Edwards and Bouvier (1897), Chace (1942), Sivertsen and Holthuis (1956), and Ambler (1980). Lack of epipods on the pereopods immediately separates *M. alvisca* from species such as *M. crassa* Smith, 1885 and *M. subsquamosa* Henderson, 1885 which it superficially resembles. Both of the latter species have relatively prominent rugae and spines on the cephalothorax and legs whereas *M. alvisca* has fairly smooth ornamentation on these body parts, except for minor development of spines on the lateral carapace margin anteriorly. The rostrum of all of these species is narrowly triangular, curves moderately upward to the tip and bears a middorsal carina, but the carina in *M. alvisca* bears almost imperceptible scalelike rugae and diminishes to obsolescence on the gastric region whereas in both *M. crassa* and *M. subsquamosa* the carina is varyingly rugose, rather strongly so in the former, and maintains this ornamentation onto the gastric region. Moreover, *M. crassa* bears tiny irregular marginal spines on the rostrum.

Spination of the merus of the third maxilliped is far weaker in *M. alvisca* than in the other two species discussed, and both the anterolateral spine of the ischium and the crenulate margin of the crest on the ischium are less developed than in them. On the other hand, *M. alvisca* possesses both mesiodorsal and mesioventral eye spines whereas *M. subsquamosa* and *M. crassa* lack the mesioventral spine.

More distant comparisons seem inappropriate because of different body proportions and ornamentation, rostral width, length, elevation and spination, and structure of the eye and third maxilliped. The keys for identification by both Chace (1942) and Pequegnat and Pequegnat (1970), for example, though strictly applicable to species of the Atlantic basin, would ally *M. alvisca* with *M. aries* (A. Milne Edwards, 1880), a much larger species with broader cephalothorax and rostrum, eyes almost hidden from dorsal view, and with less transverse ornamentation. The revised version of this key by Pequegnat and Pequegnat (1971) would place *M. alvisca* in the couplet space occupied by *M. sundi* Sivertsen and Holthuis, 1956, a species with superficially similar shaped cephalothorax, but densely clothed with short setae.

Etymology.—The name is an acronym taken from names of the deep submersible vessels used in collecting the species, *Alvin* and *Pisces IV*.

BRACHYURA: BYTHOGRAEIDAE

Bythograea mesatlantica new species

Figures 9, 10

Material.—USNM 234300, Holotype ♀, Mid-Atlantic Rift Valley about 70 km south of Kane

[2]Verena Tunnicliffe, Department of Biology, University of Victoria, P.O. Box 1700, Victor, B.C., Canada V8W 2R2, pers. commun. 1987.

Fracture Zone (see: Kong et al. [1985]; Leg 106 Shipboard Scientific Party [1986]; Ocean Drilling Program Leg 106 Scientific Party [1986]), 23°22.09'N, 44°57.12'W, 3,437 m, *Alvin* Dive 1683, MARK vent, Stn. 1, scoop, 30 May 1986, pilot D. Foster, observers S. Humphris and J. Edmond. From NSF-Leg 106-Ocean Drilling Program, NSF Grant OEC-8311201 to J. F. Grassle, Woods Hole Oceanographic Institution, Woods Hole, MA.

Measurements in mm.—

Carapace		
Length	13.8	
Width	23.3	
Depth of cephalothorax	8.1	
Frontoorbital width	7.7	
Propodus lower margin	R 15.5	L 15.2
Dactyl length	8.3	8.3
Palm		
Height	7.9	7.8
Thickness	4.9	5.1

Description.—General aspect similar to that of *B. thermydron*, cancroid, depressed. Carapace (Figs. 9, 10*d*) broad, transversely elliptical, its rounded lateral angles displaced somewhat anteriorly; almost flat in middle dorsally, very slightly arched from anterior to posterior and near lateral margins; anterolateral region produced, margin not toothed; surface finely granulate anteriorly and laterally, smooth but minutely punctate to unaided eye over posterior 2/3 to 3/4; regions indistinct. Frontoorbital width ca 1/3 carapace width.

Front almost evenly rounded and somewhat deflexed, projecting over folded antennules, shallow median depression continued onto protogastric region giving faint suggestion of bilobation; margin beaded with line of fairly uniform granules, closely packed on anterior and anterolateral parts but diminishing almost to obsolescence near orbits. Arcuate tract of scattered punctations sweeping across anterolateral, hepatic, orbital, protogastric, and metagastric regions. Transverse tract of rather prominent granules at rear edge of protogastric region. Carapace with smooth part behind these anterior areas microscopically granular and punctate anteriorly, grading posteriorly into almost featureless sur-

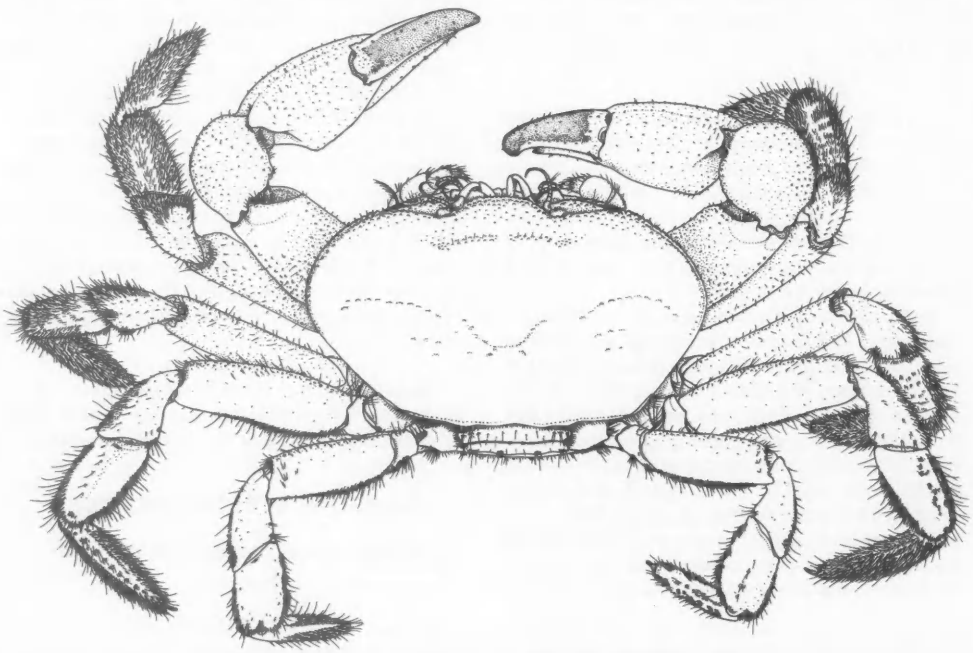

FIGURE 9.—*Bythograea mesatlantica*, holotype ♀: dorsal. Scale = 3 mm.

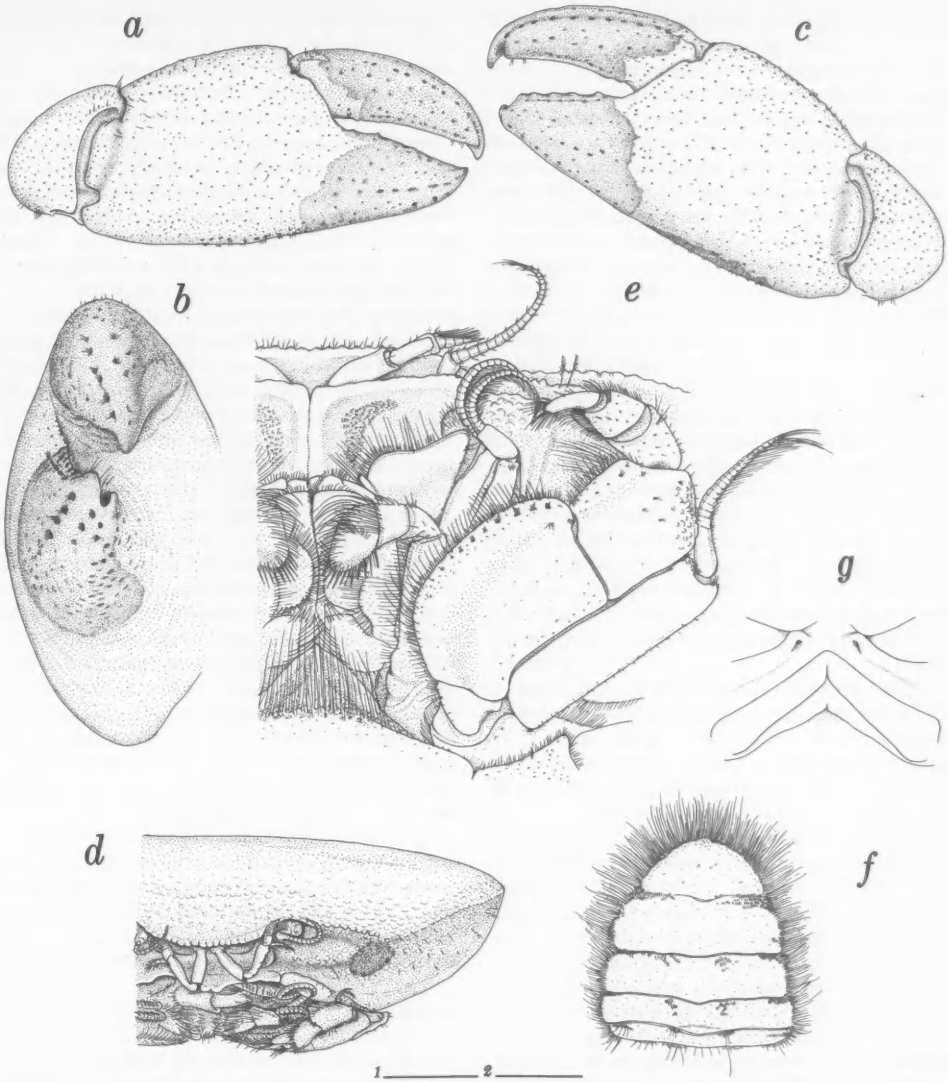

FIGURE 10.—*Bythograea mesatlantica*, holotype ♀: right chela, *a* frontal view, *b* fingers viewed from tips; *c* left chela, frontal view; *d* left side of cephalothorax in frontal view showing anterolateral pigmented spot, eye, antennules, antennae, and mouthparts in situ; *e* mouth field showing third maxilliped turned to side, second maxilliped, first maxilliped with lacinia bearing tiny "portunid lobe" at its mesial corner, partly hidden mandibles, and palate with patch of fine setae to either side of midline; *f* abdomen showing somites 3–6 and telson; *g* oviducal openings and parts of associated sternites. Scales: 1 (*a–d*, *f–g*) = 2 mm; 2 (*e*) = 1 mm.

face. Protogastric, mesogastric, metagastric, and cardiac regions poorly indicated; epibranchial line indicated by small, light colored blotches originating posterior to lateral angle at each side and arching anteromesially over branchial region, then posteromesially toward mesogastric region. Posterior margin concave and paralleled by obsolescent postmarginal groove becoming more pronounced along posterolateral margin.

Subhepatic and subbranchial areas ornamented with small granules, coarsest along upper part of hepatic region but becoming finer and more numerous near base of chelipeds.

Orbits sunk into essentially smooth transverse concavity in anterolateral region confluent laterally at either side with a prominent irregularly oval tan colored spot having very finely granulate, shallowly concave surface; somewhat inflated and irregularly granular suborbital area almost fully visible in dorsal view, reaching level of front, tilted anteroventrally from frontal plane lateral to and almost at same level as epistome.

Eyestalks projecting anterolaterad, barely movable, depressed and broadened to fit snugly in orbit; unpigmented cornea terminal, subcircular, narrower than eyestalk and anterolaterally oriented.

Epistome (Fig. 10*e*) projecting well beyond front, its anterior margin cut into 6 unequal lobes; rather narrow and advanced submedian lobes, separated by narrow deep notch, much broader intermediate lobes and somewhat less broadened lateral lobes less advanced.

Antennules folding transversely, stouter than antennae, large bulbous basal articles contiguous, concealed beneath front, interantennular septum represented by minute remnant at upper and lower edge of antennular fossa; slender penultimate and terminal articles of peduncle nearly equal in length, former slightly hollowed laterally, latter slightly longer and more slender. Flagella short; mesial 7-segmented ramus slender; slightly shorter lateral ramus curved, multisegmented, thick at base but tapering to point, dense mesial brush of long sensory setae in chord of curve.

Antennal insertion mesial to eyestalk; peduncle mesial to eyestalk, extending anteriorly or anterolaterally in situ; fixed article broad but short; first free article slender, ca 1.7 length of second article; latter broadened distally; terminal article short, its diameter only slightly greater than that of flagellar base; flagellar length exceeding midline of front.

Mouth field (Fig. 10*e*) divergent anteriorly, sides of its frame broadest posteriorly and somewhat swollen and granular at anterolateral corners, maximal inside anterior width about 1.4 minimal inside posterior width. Third maxillipeds filling mouth field except for narrow gap of nearly uniform width between ischia of endognaths and rather irregular gap anteriorly between meri-carpi of endognaths and epistome; exognaths overlapping sides of mouth frame. Endognaths with exposed surface bearing sparse, sometimes linear, setose punctations; exposed surface of ischium nearly smooth; elongate polygonal in outline but primarily rectangular, greatest (distal) width 1.1 narrowed part ca 1/2 length from base; mesial margin straight through most of its length but curved at each end, toothless, bearing many stiff straight setae, submarginal zone somewhat thickened and flanked laterally by shallow longitudinal groove; anterior margin nearly perpendicular to mesial margin except for anteriorly projecting truncate lobe at inner corner; lateral margin concave; posteromesial margin obliquely convex; basi-ischial suture line visible posterolaterally. Merus slightly narrower than ischium; low granules with tips directed anteromesially along distal margin; irregularly quadrate perimeter flanked by submarginal thickened zone and groove similar to mesial counterpart on ischium except on straight proximal side, anterolateral angle broadly rounded, anteromesial angle at insertion of palp oblique; mesial margin doubled anteriorly for reception of folded palp, its ventral (exposed) side broadly angled proximal to carpopropodal articulation; posteromesial corner fitted to projecting lobe of ischium, dorsal (hidden) side produced behind carpus, its margin setose. Palp large, dactyl reaching posteriorly about 1/4 length mesial margin of ischium. Carpus expanded distally, narrowed proximally, bent nearly at right angle near insertion and obscurely crimped inside angle; dense tuft of setae on distooral surface. Propodus wider than carpus, longer than broad, asymmetrically ovate in ventral view; distal (longest) margin convex, densely beset with rows of strong serrated setae, longest distally; distal tuft of such setae on dorsal surface. Linear dactyl slightly bent away from midline in distal part and setose as propodus, especially on prehensile edge. Exognath narrow, not extending to full length of merus; ventral surface slightly curved mesially to fit closely against lateral side of endognathal ischium, with dorsomesial flange (widest distally)

fitting beneath latter; palp conspicuous, flagellum densely beset with setae in hollow of curve.

First maxilliped with lacinia of endopod broad, its distal edge 3-lobed and conspicuously though not heavily setose; oblique mesial margin of strongly advanced anterolateral lobe confluent with broader gradually rounded and much less advanced intermediate lobe, latter in turn followed by still less advanced tiny mesial lobe, separated by a notch and directed anteromesially; tuft of setae preceding notch.

Endostome large, divided by low median sagittal ridge bifurcated somewhat anteriorly and merging into projecting endostome; each half of palate shallowly concave, crossed by low longitudinal ridge slightly offset at its midlength and trending anteromesially from near base of large mandibular palp; ridge flanked laterally by irregular patch of velvety pubescence; smooth lateral 2/3 of palate receiving large efferent branchial channels.

Chelipeds (Figs. 9, 10*a*, *b*, *c*) heavy, subequal; integument punctuate on upper and extensor surfaces, obscure granulation on upper surfaces of palms and on ridges or raised areas elsewhere; chelae inflated, lower margin of palm arched downward, its rather pronounced keel merging into fixed finger; swollen palm with shallow excavation proximally for reception of carpus in flexed position, inner surface glabrous but drawn into moderate and slightly granular elevation slightly in front of proximal excavation. Fingers tan colored in preservation (70% ethanol) and darkest proximally, color of fixed finger not extending onto palm; fingers not gaping, prehensile edges entire except for obsolescent proximal tooth on fixed finger of each hand; dactyl longer than relatively straight fixed finger, arching down distally to close in distal notch of spooned tip of fixed finger.

Carpus with extensor surface inflated, right carpus with internal margin rounded, that of left obscurely angled. Merus broadened mesially into cristate flange angled distally for reception of carpus, strong granules in single line along inner margin, outer surface rounded, strewn with obsolescent punctations and granules, latter most prominent along distoventral tract.

Walking legs rather long, flattened, length decreasing posteriorly in order 3, 2, 1, 4; each with dense patches of short darkened setae interspersed with sparer longer setae on extensor surface of carpus and propodus (as well as its lateral side on legs 1 and 2), distoventral corner of carpus, and more extensively on dactyl; fifth legs somewhat more flattened than others, propodi relatively broader and not densely setose laterally. Mean maximum length of propodi about twice width. Dactyls slightly longer than propodi, narrowly lanceolate, shallow longitudinal grooves on anterior and posterior surfaces obscured by dense setae, tip stout, corneous. Merus of each with upper margin finely granular, anterior lower margin present throughout length but posterior lower margin obsolescent proximally.

Sternum broadest between legs 1 and 2, narrower posteriorly, glabrous beyond outline of abdomen.

Abdomen (Fig. 10*f*) ovate in outline, fully segmented and densely fringed with plumose setae; somite 1 slightly arched dorsally to fit contour of adjacent carapace, somites 2–4 of about equal length, somites 5 and 6 progressively longer; abdomen with greatest width at 4; telson nearly as broad as somite 6, outline broadly arched distally. Somites 2–5 bearing large, well-developed biramous pleopods, outer curved branch lying near edge of abdomen and heavily beset with short setae laterally and mesially, inner branch more sparsely equipped with ovigerous setae and jointed.

Female openings (Fig. 10*g*) large, obscurely subtriangular in outline.

Color in preservation predominantly off-white except for fingers, matted setal tracts laden with brownish finely particulate matter.

Remarks.—Brachyuran crabs that resemble *Bythograea* were observed and reported by Rona et al. (1986).

Bythograea mesatlantica differs in several respects from Pacific members of the genus, *B. thermydron* Williams (1980) and *B. microps* de Saint Laurent (1984). Among obvious differences from *B. thermydron*, the new species has even less ornamentation on the carapace; it lacks a distinct suborbital plate separated by a suture, and the suborbital area is inflated, not flat and inclined; there is a transverse concavity lateral to each eyestalk that terminates near the very distinctive brown spot in the cuticle at either side of the carapace; the eyestalk itself is shorter and thicker than in *B. thermydron* and the shape and position of the cornea differs. The ischium of the third maxilliped is relatively shorter than in *B. thermydron* and bears only sparse setiferous punctations on the external surface, it lacks tiny granules on the truncate lobe at the anterolateral

corner, the submarginal thickened zone and groove are less distinct; the merus is not tilted dorsally in normal position, and the palp is relatively shorter and club shaped rather than curved like a knife edge along the prehensile edge. The lacinia of the first maxilliped is more angular anterolaterally and has a smaller "portunid lobe". The epistome is less lobulate than in *B. thermydron* and the concave palatal area has much less setose covering. The nearly toothless chelae have brown fingers and there is no dense patch of setae on the inner side of the palms.

Comparisons with *B. microps* are necessarily less complete because of the brief description of the latter. The eyes are certainly not slender and retracted in *B. mesatlantica*; the chelipeds are not noticeably dimorphic, and they are relatively smooth rather than strongly granular and pilose on the external surface as in *B. microps*.

The distinctive exocular spots on the carapace seem similar to those noted on the chelipeds of *Hypsophrys noar* Williams (1974, 1976) and *Munidopsis lentigo* (Williams and Van Dover 1983). Their function is unknown.

Etymology.—From the Greek "mesos", middle and "Atlantic", with reference to the Mid-Atlantic Rift habitat.

ACKNOWLEDGMENTS

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LITERATURE CITED

AMBLER, J. W.
1980. Species of *Munidopsis* (Crustacea, Galatheidae) occurring off Oregon and in adjacent waters. Fish. Bull., U.S. 78:13–34.

ASHES EXPEDITION.
1986. *Pisces* submersible exploration of a high-temperature vent field in the caldera of Axial Volcano, Juan de Fuca Ridge. Eos 67(44):1027.

BROOKS, J. M., M. C. KENNICUTT II, C. R. FISHER, S. A. MACKO, K. COLE, J. J. CHILDRESS, R. R. BIDIGARE, AND R. D. VETTER.
1987. Deep-sea hydrocarbon seep communities: Evidence for energy and nutritional carbon sources. Science 238:1138–1142.

CANADIAN AMERICAN SEAMOUNT EXPEDITION.
1985. Hydrothermal vents on an axis seamount of the Juan de Fuca Ridge. Nature 313:212–214.

CHACE, F. A., JR.
1942. Reports on the scientific results of the Atlantis expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. The Anomuran Crustacea. I. Galatheidae. Torreia, Havana, 11:1–106.

CHILDRESS, J. J., C. R. FISHER, J. M. BROOKS, M. C. KENNICUTT II, R. BIDIGARE, AND A. E. ANDERSON.
1986. Methanotrophic marine molluscan (Bivalvia, Mytilidae) symbiosis: mussels fueled by gas. Science 233:1306–1308.

DE SAINT LAURENT, M.
1984. Crustacés Décapodes d'un site hydrothermal actif de la dorsale du Pacifique oriental (13° Nord), en provenance de la campagne française Biocyatherm. C. R. Hebd. Séances Acad. Sci. Ser. 3 Sci. Nat. (Paris) 299(9):355–360, plate 1.

KONG, L., W. B. F. RYAN, L. A. MAYER, R. S. DETRICK, P. J. FOX, AND K. MANCHESTER.
1985. Bare-rock drill sites, O.D.P. Legs 106 and 109; evidence for hydrothermal activity at 23°N on the Mid-Atlantic Ridge. EOS 66(46):936.

LEG 106 SHIPBOARD SCIENTIFIC PARTY (R. S. Detrick, J. Honnorez, A. C. Adamson et al.).
1986. Mid-Atlantic bare-rock drilling and hydrothermal vents. Nature 321:14–15.

MILNE EDWARDS, A.
1880. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and in the Caribbean Sea, 1877, '78, '79, by the United States Coast Survey Steamer "Blake," . . . . VIII.—Études préliminaires sur les Crustacés. Bull. Mus. Comp. Zool. Harvard 8:1–68, 2 plates.

MILNE EDWARDS, A., AND E. L. BOUVIER.
1897. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78), in the Caribbean Sea (1878–79), and along the Atlantic coast of the United States (1880), by the U.S. Coast Survey Steamer *"Blake,"* . . . . XXXV. Description des Crustacés de la famille des Galathéidés recuellis pendant l'expédition. Mem. Mus. Comp. Zool. Harvard 19:1–141.

OCEAN DRILLING PROGRAM LEG 106 SCIENTIFIC PARTY.
1986. Drilling the Snake Pit hydrothermal sulfide deposit on the Mid-Atlantic Ridge, lat 23°22'N. Geology 14(12):1004–1007.

PEQUEGNAT, L. H., AND W. E. PEQUEGNAT.
1970. Deep-sea anomurans of Superfamily Galatheoidea with descriptions of two new species. *In* W. E. Pequegnat and F. A. Chace (editors), Contributions on the biology of the Gulf of Mexico. Tex. A&M Univ. Oceanogr. Stud. 1(5):125–170.

PEQUEGNAT, W. E., AND L. H. PEQUEGNAT.
1971. New species and new records of *Munidopsis* (Decapoda: Galatheidae) from the Gulf of Mexico and Caribbean Sea. Contributions on the biology of the Gulf of Mexico. Tex. A&M Univ. Oceanogr. Stud. 1 (Suppl.):1–24.

RONA, P. A., G. KLINKHAMMER, T. A. NELSON, J. H. TEFREY, AND H. ELDERFIELD.
1986. Black smokers, massive sulphides and vent biota at the Mid-Atlantic Ridge. Nature 321:33–37.

SAINT LAURENT, M., DE. *See* De Saint Laurent.

SIVERTSEN, E., AND L. B. HOLTHUIS.

1956. Crustacea Decapoda (The Penaeidea and Stenopodidea excepted). Rep. Sci. Results "Michael Sars" North Atl. Deep-Sea Exped. 1910, 5(12):1–54, plates 1–4.

TUNNICLIFFE, V., M. BOTROS, M. E. DE BURGH, A. DINET, H. P. JOHNSON, S. K. JUNIPER, AND R. E. MCDUFF.

1986. Hydrothermal vents of Explorer Ridge, northeast Pacific. Deep-Sea Res. 33:401–412.

TUNNICLIFFE, V., S. K. JUNIPER, AND M. E. DE BURGH.

1985. The hydrothermal vent communities on Axial Seamount, Juan de Fuca Ridge. Bull. Biol. Soc. Wash. 6:453–464.

VAN DOVER, C. L., B. FRY, J. F. GRASSLE, S. HUMPHRIS, AND P. A. RONA.

In press. Feeding biology of the Mid-Atlantic Ridge hydrothermal vent shrimp: Functional morphology, gut content analyses, and stable isotopic composition. Mar. Biol. (Berl.).

WILLIAMS, A. B.

1974. A new species of *Hypsophrys* (Decapoda: Homolidae) from the Straits of Florida, with notes on related crabs. Proc. Biol. Soc. Wash. 87:485–492.

1976. Integumental organs of unknown function on chelipeds of deep-sea crabs, genus *Hypsophrys*. J. Morphol. 150:889–900.

1980. A new crab family from the vicinity of submarine thermal vents on the Galapagos Rift (Crustacea: Decapoda: Brachyura). Proc. Biol. Soc. Wash. 93:443–472.

WILLIAMS, A. B., AND F. A. CHACE, JR.

1982. A new caridean shrimp of the family Bresiliidae from thermal vents of the Galapagos Rift. J. Crust. Biol. 2:136–147.

WILLIAMS, A. B., AND P. A. RONA.

1986. Two new caridean shrimps (Bresiliidae) from a hydrothermal field on the Mid-Atlantic Ridge. J. Crust. Biol. 6:446–462.

WILLIAMS, A. B., AND C. L. VAN DOVER.

1983. A new species of *Munidopsis* from submarine thermal vents of the East Pacific Rise at 21°N (Anomura:Galatheidae). Proc. Biol. Soc. Wash. 96:481–488.

THE MEGALOPA STAGE OF THE GULF STONE CRAB, *MENIPPE ADINA* WILLIAMS AND FELDER, 1986, WITH A COMPARISON OF MEGALOPAE IN THE GENUS *MENIPPE*

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ABSTRACT

The laboratory-reared megalopa stage of the Gulf stone crab, *Menippe adina*, is described and illustrated and compared with megalopae of three other species of *Menippe*. The megalopa of *M. adina* differs from that of *M. nodifrons* in having serrate spines on the ventral margin of the dactylus of pereiopod 5 and from that of *M. rumphii* in having spines on the dactyli of pereiopods 2–5 and a more quadrate carapace. The megalopa of the morphologically similar *M. mercenaria* was also reared in the laboratory, and selected characters are described and compared with the megalopa of *M. adina*; megalopae of the two species differ only slightly. Megalopae of *M. adina* taken from field collections made off South Texas, U.S.A., were compared with and were found to be consistent with laboratory-reared *M. adina* megalopae.

Stone crabs of the genus *Menippe* are large xanthid crabs common along the eastern coasts of the United States and Mexico from North Carolina to Yucatan, the Bahamas, Cuba, and Jamaica (Rathbun 1930; Felder 1973; Williams 1984; Williams and Felder 1986). Recently the "common" stone crab, *Menippe mercenaria* (Say, 1818), was divided into two species: *Menippe mercenaria* (Say) (restricted), known from the east coast of the United States, the Caribbean, and the west coasts of Florida and Yucatan, and *Menippe adina* Williams and Felder, 1986, known from the northwestern Gulf of Mexico; hybridization of the two species occurs in northwest Florida (see Williams and Felder 1986). These two species (primarily *M. mercenaria*) support an important stone crab fishery in the southern United States and Mexico (Williams and Felder 1986) and consequently have been the subject of numerous investigations. Despite this interest, the complete larval developments of both commercial species of *Menippe* remain unknown. For *M. mercenaria* (Say), Hyman (1925) described a prezoea and first zoeal stage, and Porter (1960) described six zoeal stages reared in the laboratory. Unfortunately, Porter did not describe the megalopa stage, presumably because he considered it a postlarva and not a true larval stage. An unpublished but often-cited report by Kurata[4] included descriptions of the zoeal stages of *M. mercenaria* and a brief sketch of the megalopa; Kurata's description of the megalopa did not include morphology of the pleopods, pereiopods, or mouthparts.

Because of recent interest in the phylogenetic significance of the brachyuran megalopa (see Rice 1981a, in press; Martin in press) and postlarval stages (Martin et al. 1984; Felder et al. 1985), and because of the potential importance of stone crab larval biology to aquaculture, it is surprising that the megalopae of *M. mercenaria* and *M. adina* remain undescribed. The present paper describes the laboratory-reared megalopa of the Gulf stone crab, *Menippe adina* Williams and Felder, and compares it with field collections of the same species from south Texas, laboratory-reared megalopae of *M. mercenaria*, and all previously described megalopae of the genus *Menippe: Menippe mercenaria* (Say, 1818) (as described by Kurata fn. 4); *Menippe nodifrons* Stimpson, 1859 (as described by Scotto 1979); and *Menippe rumphii* (Fabricious, 1798) (as described by Kakati 1977).

MATERIALS AND METHODS

A large ovigerous *M. adina* was collected from

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[4]Kurata, H. 1970. Studies on the life histories of decapod Crustacea of Georgia. Part III. Larvae of decapod Crustacea of Georgia. Unpubl. rep., 274 p. University of Georgia Marine Institute, Sapelo Island, GA.

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shallow waters of the northern Gulf of Mexico near Grande Terre, LA, in May 1982 and held in a small aquarium at room temperature. After the eggs hatched, the zoeal larvae were given fresh seawater and newly hatched *Artemia* nauplii daily. Exuviae as well as dead and some living megalopae were preserved in 70% ethanol. Drawings were made with the aid of a Wild[5] M-5 stereoscope and a Wild M-11 compound stereoscope, both with camera lucida; accuracy was verified with a Nikon Optiphot. Measurements were made with an ocular micrometer. Ten laboratory-reared megalopae were examined, measured, dissected, and compared with megalopae from field collections made in 1973 off south Texas. Comparisons with *M. mercenaria* are based on laboratory-reared *M. mercenaria* megalopae from two females collected on 13 August 1987 from the Indian River system, north of Ft. Pierce, FL. Eggs of these two females hatched on 21 August 1987, and the megalopa stage was first reached after 17 days in mass culture aquaria (30‰ salinity, 25°C, 12h:12h light/dark regime). Descriptions of setation for all appendages proceed from proximal to distal. Specimens examined under the scanning electron microscope (SEM) were prepared according to procedures outlined by Felgenhauer (1987) but without postfixation in osmium tetroxide and with 100% ethanol, rather than amyl acetate, as the transitional fluid. Sibling megalopae and field collections have been deposited in the U.S. National Museum of Natural History, catalogue No. USNM 229962 (laboratory-reared *M. adina*), USNM 229961 (field-collected *M. adina*), and USNM 229963 (laboratory-reared *M. mercenaria*).

RESULTS

Carapace (Figs., 1A, B, C, 3A).—Length 1.67 mm, width 1.45 mm (N = 10). Subquadrate, with 2 lateral prominences on each side; dorsoventrally thick, with minute tubercle centrally located. Posterior border fringed with numerous short setae; lateral margin with few scattered setae. Rostrum ventrally deflexed, nearly vertical, with deep medial depression, rounded anteriorly. Angular interorbital prominences extend ventrally between orbit and antennule. Chromatophores variable in placement, but almost always found in areas indicated in Figure 1B.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Eyes (Figs. 1A, B, C, 3A).—Large, exposed; eyestalks sometimes with 2 or 3 short, simple anterior setae, always with posterodorsal chromatophore.

Abdomen (Fig. 1A, B).—Subequal in length to carapace. All pleura with rounded posterolateral angles. All somites with sparse setae dorsally; somites 2–5 always with elongated chromatophores.

Telson (Fig. 1G).—Broadly rounded with variable setation, occasionally with pair of small posterior spines (as in Figure 1B).

Antennule (Fig. 1K).—Biramous; peduncle 3-segmented, with variable setation. Basal segment of peduncle large, bulbous, always with large chromatophore; middle segment subcylindrical with 0–2 distal setae; distal segment ovoid with scattered short setae. Lower ramus 1-segmented with 6–8 setae; upper ramus 5-segmented with aesthetascs arranged in tiers, usually 0, 7, 8, 6, 4 subterminal plus 3 terminal, with short setae sometimes present on segments 2 and 4 (note: all aesthetascs not illustrated).

Antenna (Fig. 1J).—Flagellum 12-segmented (sometimes 11), with 3 peduncular articles and 8 or 9 flagellar articles (see Rice, in press, for correct number of antennal segments in megalopae); setation variable, usually 2, 3, 2, 0, 0, 2, 4, 0, 4 or 5, 1, 4, 4.

Mandibles (Fig. 2F).—Asymmetrical, with broadly rounded spade-shaped cutting edges; palp 2-segmented with setation 0, 11–14.

Maxillule (Fig. 2E).—Protopodite with 1 or 2 long plumose setae on posterodorsal margin; endopodite 2-segmented with setation 1, 2 subterminal plus 2 terminal; basal endite with 29–35 spines and setae; coxal endite with 13–16 spines and setae.

Maxilla (Fig. 2D).—Scaphognathite with 70–78 fringing setae and 0–6 setae on blade; endopodite unsegmented with 0 or 1 distolateral seta and 4 or 5 basal plumose setae; basal endite bilobed with setation variable, usually 8–10, 9–11; coxal endite bilobed with setation usually 7, 9 or 10.

Maxilliped 1 (Fig. 2C).—Exopodite 2-segmented, with setation 2 or 3, 5–7. Endopodite

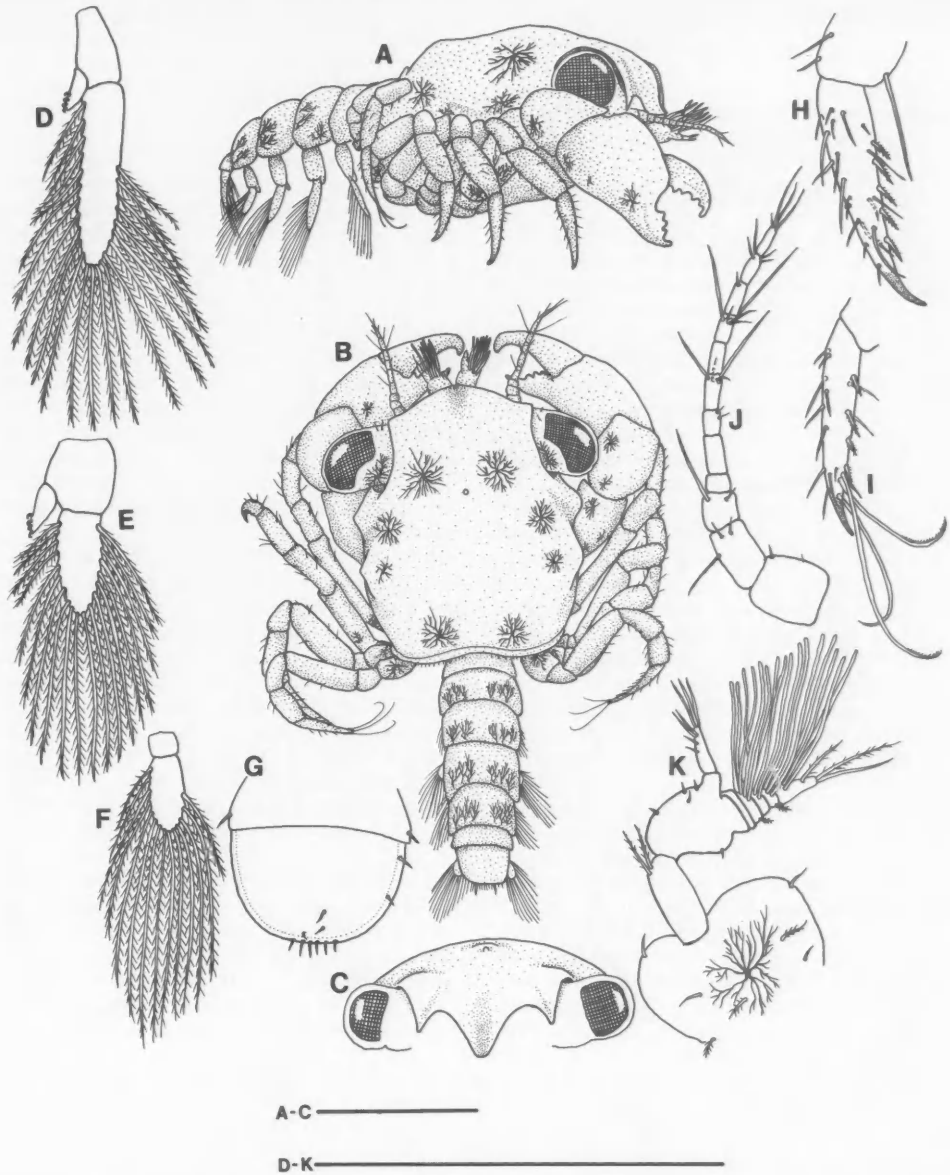

FIGURE 1.—Megalopa of the Gulf stone crab, *Menippe adina*. A, entire animal, lateral view; B, same, dorsal view; C, frontal view of rostrum and eyes; D, pleopod 1; E, pleopod 4; F, pleopod 5; G, telson and posterior part of sixth abdominal segment; H, dactylus of pereiopod 3; I, dactylus of pereiopod 5; J, antenna; K, antennule, Both scale bars = 1.0 mm.

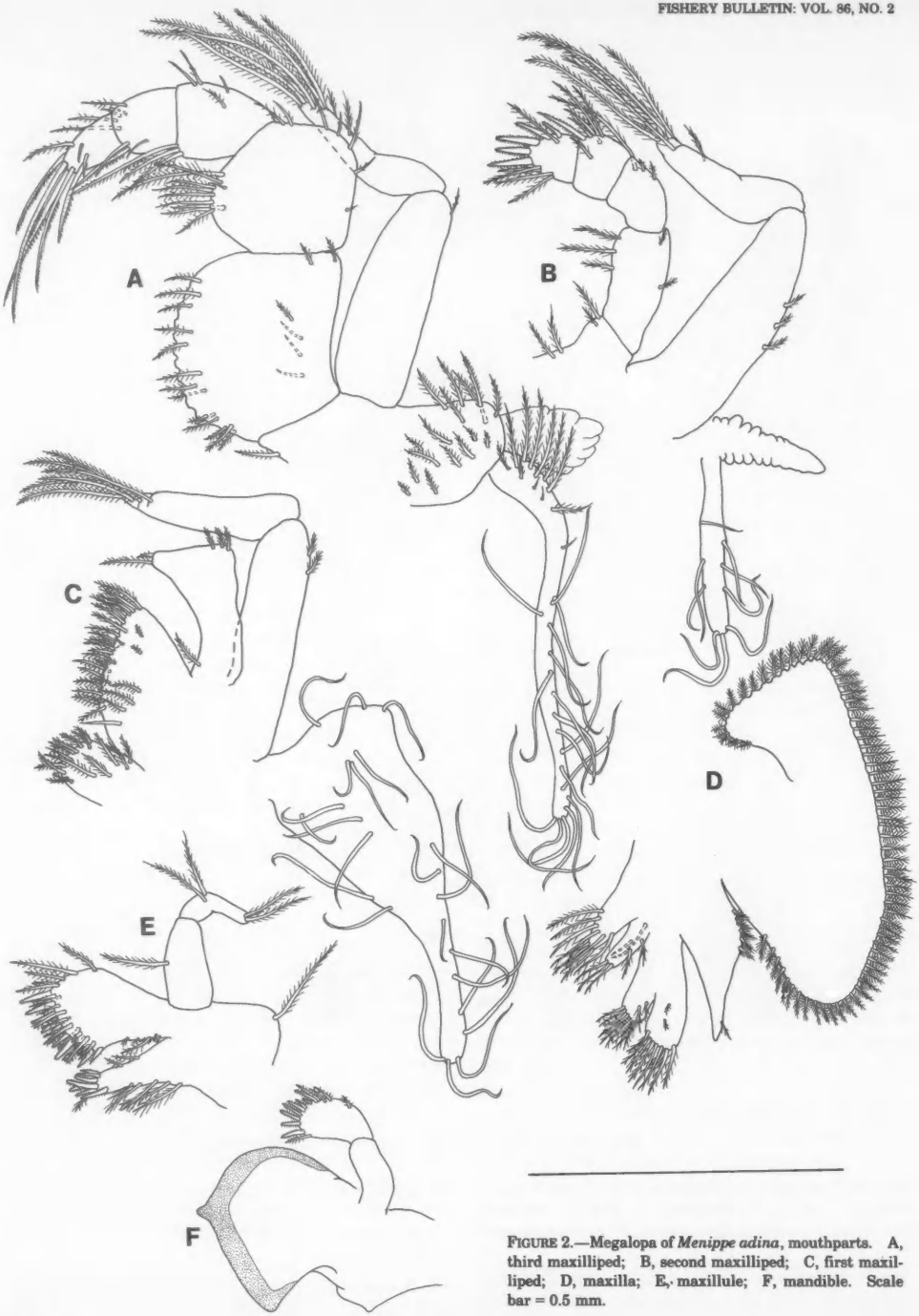

FIGURE 2.—Megalopa of *Menippe adina*, mouthparts. A, third maxilliped; B, second maxilliped; C, first maxilliped; D, maxilla; E, maxillule; F, mandible. Scale bar = 0.5 mm.

unsegmented with 6–8 setae arranged as shown. Basal endite setation 28–33; coxal endite setation 15–17. Epipodite with 22 or 23 long, minutely plumose setae, appearing simple under low magnification.

Maxilliped 2 (Fig. 2B).—Exopodite 2-segmented, with setation 3, 5–8. Endopodite 4-segmented, with setation usually 5, 2 or 3, 5 or 6, 9 or 10; distal segment with 4 or 5 stout serrate setae. Epipodite with 9 or 10 long minutely plumose setae.

Maxilliped 3 (Fig. 2A).—Exopodite 2-segmented, with setation 0 or 1, 6–8. Endopodite 5-segmented, with variable setation, usually 18–20, 15 or 16, 5–9, 6–8, 7–10; ischium with scalloped medial border. Epipodite with 18 long minutely plumose setae on distal two-thirds plus 8–12 plumose setae on proximal one-third. Protopodite setation variable.

Pereiopods (Figs. 1A, B, H, I, 3B, C, D).—Chelipeds long, stout, subequal; dactylus with 4 irregular teeth; immovable finger with 3 teeth (Fig. 3B); tips of fingers overlap distally when approximated. No recurved hook on basi-ischium (Fig. 3B). Second to fourth pereiopods similar; dactylus with 5 (rarely 4) serrate spines ventrally (e.g., Figs. 1H, 3C, D); propodus with long ventrodistal spine (Fig. 1H). Fifth pereiopod dactylus (Fig. 1I) with 3 long pectinate setae, 1 markedly toothed and concave (Fig. 3E), on distal ventral border and 3 or 4 serrate spines ventrally.

Pleopods (Fig. 1D, E, F).—Decreasing in size posteriorly. Pleopod 1 (Fig. 1D) with 19–22 plumose setae; endopodite with 3 or 4 hooked setae. Pleopod 4 (Fig. 1E) with 19–21 plumose setae; endopodite with 3 or 4 hooked setae (Fig. 3F). Pleopod 5 (uropod) (Fig. 1F) with 12–14 plumose setae; basal segment lacking setae or with 1 or 2 setae (field collections); endopodite absent.

Color.—Overall coloration rose-orange, with dark blue-black chromatophores located as shown in Figure 1A, B.

DISCUSSION

The genus *Menippe* de Haan, 1833, presently contains about 8 species, only 3 of which occur in North America. The megalopa stage is now known for 3 species in the genus: *M. rumphii* (Fabricious, 1798), *M. nodifrons* Stimpson, 1859, and *M. adina* Williams and Felder, 1986. In addition, selected characters of *M. mercenaria* (Say, 1818) are presented here for comparison; some characters of that species are also obtainable from an unpublished report by Kurata (fn. 4) (see Table 1).

Laboratory-reared megalopae of *M. adina* were virtually identical to megalopae presumed to belong to *M. adina* that were collected off south Texas. Even meristic counts of the mouthpart setation agreed exactly, with the only observed differences being that field-collected megalopae were slightly larger and occasionally bore 1 or 2 setae on the basal segment of the uropod. Thus, we feel that our laboratory conditions have not adversely affected development or introduced abnormal characters, and we have used these field collections for the SEM figures of *M. adina* megalopae (Fig. 3).

We expected to find that characters of the megalopa of *M. adina* are similar to those described by Kurata (fn. 4) for the morphologically similar (in adulthood) *M. mercenaria*, a species known to hybridize with *M. adina* (see Williams and Felder 1986). In general this is true. However, some characters reported by Kurata differ from our observations on *M. adina* and from our laboratory-reared megalopae of *M. mercenaria* (Fig. 4). Kurata mentioned (but did not illustrate)

TABLE 1.—Comparison of characters in megalopae of the genus *Menippe*. Dash (—) indicates information not available from reference.

	Size[1] (mm)		Setation				Spination			
			Palp of	Epipod of			Dactylus of		Setation	
Menippe	CL	CW	mandible	Maxilliped 1	Maxilliped 2	Maxilliped 3	Pereiopods 2–4	Pereiopod 5	pleopod 5	Reference
adina	1.67	1.45	0, 11–14	22–23	9–10	18	5	4	12–13	Present study
mercenaria	1.70	1.55	0, 11–13	20–23	7–10	18–20	4	4	11–13	Present study
mercenaria	1.7–8	—	—	—	—	—	4–5	0	11–12	Kurata[3]
nodifrons	1.50	1.31	0, 10–13	12–20, [2]26	up to 10	18	5	0	11	Scotto 1979
rumphii	1.60	1.55	0, 0, 9	22	8	18	0	0	12	Kakati 1977

[1]CL = carapace length; CW = carapace width.
[2]From a megalops hatched from a stage 6 (rather than the typical stage 5) zoea.
[3]See text footnote 4.

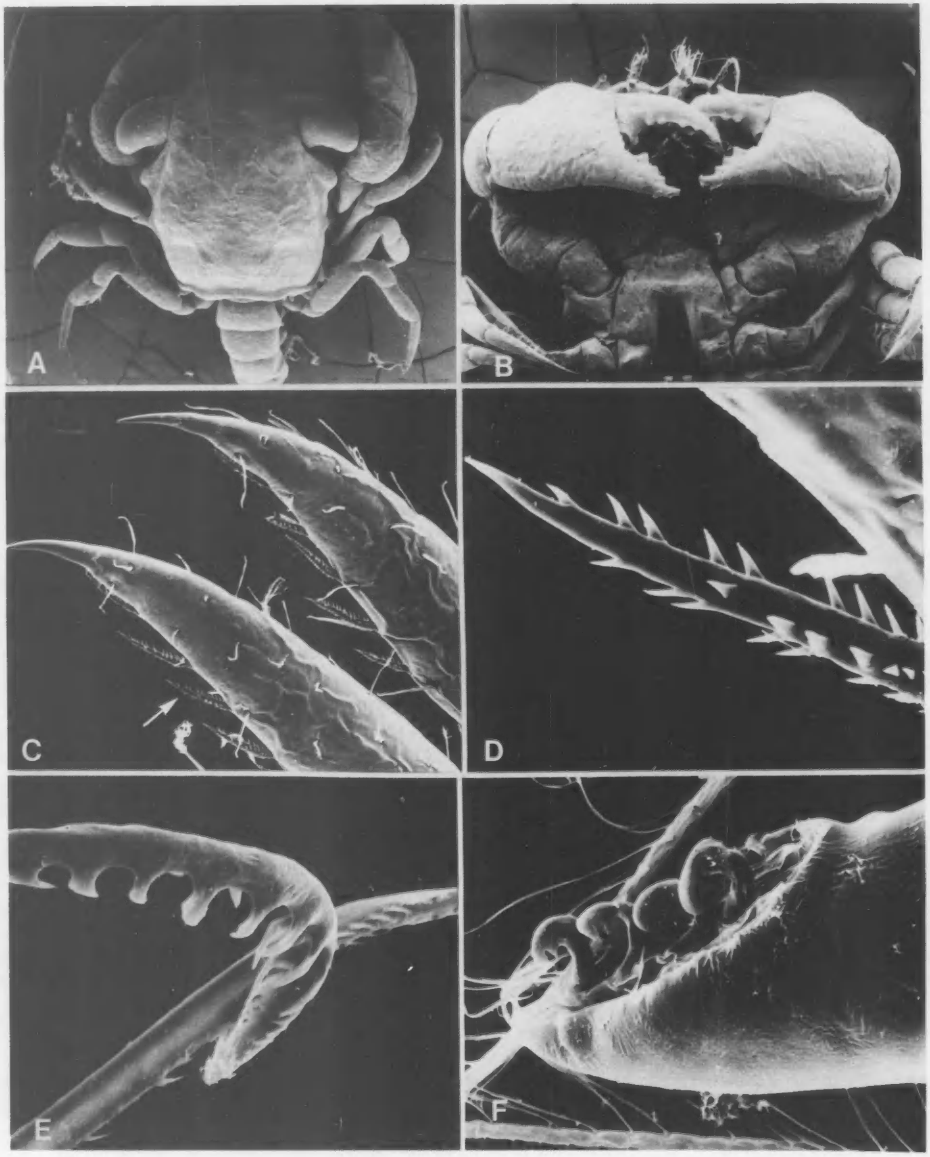

FIGURE 3.—Scanning electron micrographs (SEM) of selected characters of *Menippe* megalopae (presumably *M. adina*) collected in south Texas. A, dorsal view of carapace (× 25); B, ventral view of chelipeds showing dentition of the fingers and lack of recurved hook on ischium (× 37); C, dactyli of second (upper figure) and third pereiopods (× 230); D, higher magnification of ventral dactylar spine indicated by arrow in C (× 1,900); E, endopod of third abdominal pleopod showing 4 dentate hooklike setae (× 2,200); F, serrate setae (only 2 of 3 shown) of dactylus of pereiopod 5 (× 2,300).

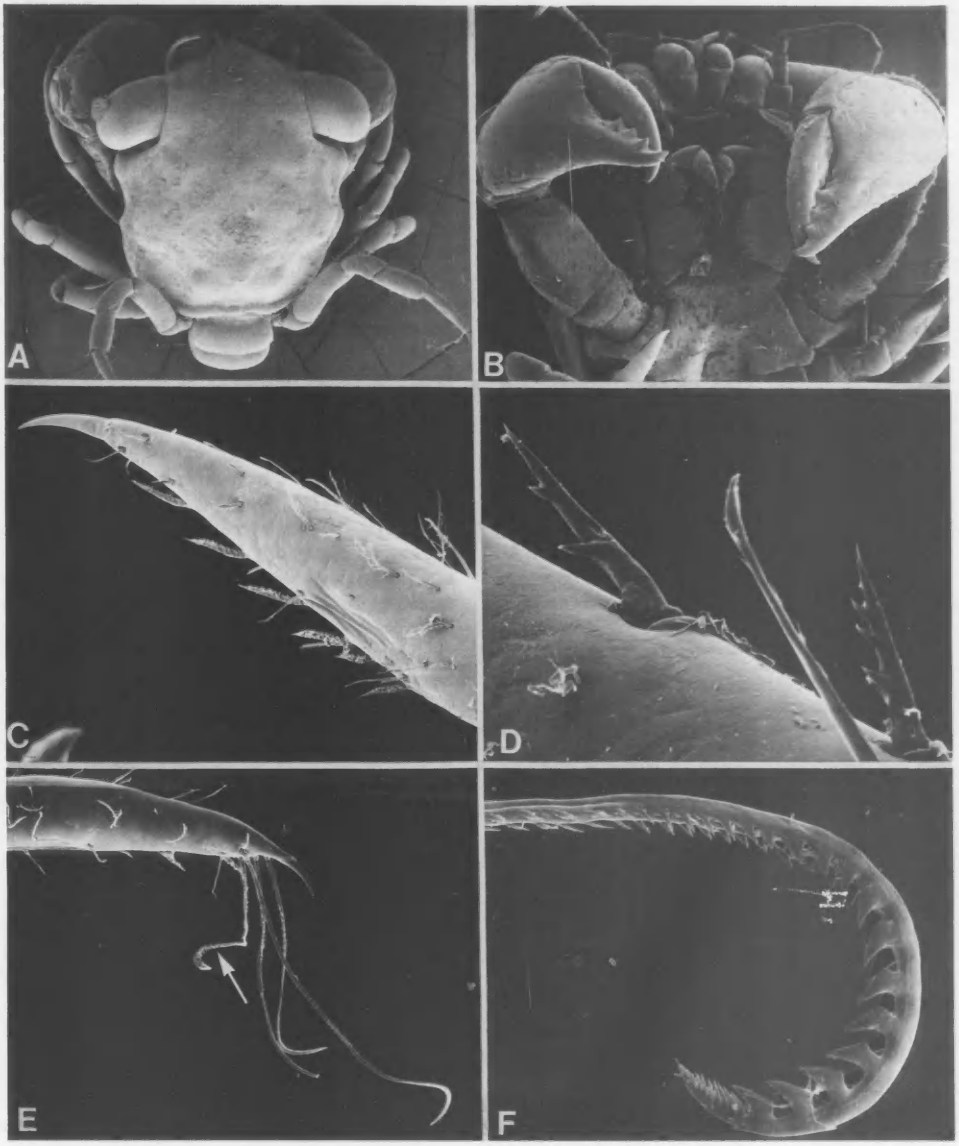

FIGURE 4.—Scanning electron micrographs (SEM) of selected characters of the laboratory-reared megalopa of *Menippe mercenaria*. A, dorsal view of carapace (× 37); B, ventral view of chelipeds and third maxillipeds (× 55); C, dactylus of second pereiopod showing ventral serrate spines (× 270); D, ventral spines on dactylus of fourth pereiopod with fewer spinules than anterior pereiopod spines (× 2,000); E, dactylus of fifth pereiopod showing four serrate "sensory" setae with one (arrow) more obviously serrate (× 190); F, higher magnification of concave serrate setae indicated by arrow in E (× 1,500).

"about 9 small spines" on the ischium of the third maxilliped; we found no spines on *M. adina* or *M. mercenaria* (Figs. 3B, 4B), but it is possible that Kurata was referring to the acute borders of the scalloped medial margin (our Figure 2A), in which case the 2 species are similar. Spination of the ischium of pereiopods 1–3 differs also; Kurata described 5 or 6, 2 or 3, and 1 small spine on the ischia of pereiopods 1, 2, and 3, respectively, whereas we did not notice this condition in *M. adina* or *M. mercenaria* (see Figures 3B, 4B). Finally, Kurata (fn. 4: pl. 74, fig. E) illustrated no spines on the ventral surface of the fifth pereiopod dactylus of *M. mercenaria*; these spines are obvious on both species (Figs. 1I, 4E). We found few differences between megalopae of *M. adina* and *M. mercenaria*. General morphology of the carapace and chelipeds, spination of the dactylus of the pereiopods, and setation of the pleopods agreed almost exactly (compare Figures 3 and 4). Ventral dactylar spines on the posterior walking legs of *M. mercenaria* were not so serrate as in *M. adina* and were sometimes armed with only 2 or 3 large spinules rather than the numerous spinules seen in *M. adina* (e.g., Fig. 3D) and in the more anterior legs of *M. mercenaria* (see Figure 3C, D, 4C). Also, in all but 1 of the 9 megalopae of *M. mercenaria* examined there were 4 (rather than 3) long serrate setae on the dactylus of the fifth pereiopod (Fig. 4E). As in *M. adina*, one of these setae was more serrate and concave than were the other long setae (Fig. 4E, F). However, we have not examined mouthpart morphology of *M. mercenaria* in the detail in which we described *M. adina*, and so it is possible that additional characters will be found to separate these 2 species at the megalopa stage.

The megalopa of *M. adina* is very similar to that of *M. nodifrons* as described by Scotto (1979). Although the 2 species differ in setation of some of the mouthparts, this setation may differ from side to side in a given individual. The salient character that serves to separate megalopae of these 2 species is the presence in *M. adina* of 4 stout serrate spines on the dactylus of pereiopod 5. Scotto (1979) figured only setae (and no spines) on the dactylus of the fifth pereiopod in *M. nodifrons* and the dactylar spines on other pereiopods apparently are not serrate (Scotto 1979, fig. 9c, pereiopod 3).

The megalopa of *M. rumphii* described by Kakati (1977) differs from that of *M. nodifrons*, *M. mercenaria*, and *M. adina* in having a more ovoid carapace with the rostrum only slightly deflexed. Kakati did not describe the dactyli of pereiopods 2–5 for *M. rumphii*, but his figure of pereiopod 2 (1977:639, fig. 2, p. 50) does not show stout ventral spines on the dactylus. Possibly Kakati overlooked these spines; if not, the absence of these spines on pereiopod 2 would further serve to separate the megalopa of *M. rumphii* from those of *M. nodifrons*, *M. mercenaria*, and *M. adina*. All 4 species have been described as having a rose-orange coloration in life.

Although Rathbun (1930) and Monod (1956) synonymized *M. rumphii* with *M. nodifrons*, descriptions of the zoeal stages of *M. rumphii* and *M. nodifrons* by Kakati (1977) and Scotto (1979), respectively, show that larvae of the 2 species differ considerably. In the first zoeal stage, *M. rumphii* exhibits elongated posterolateral processes on abdominal segment 5 that extend posteriorly to more than half the length of the telsonal furcae, which lack spines. The first zoea of *M. nodifrons* has similar posterolateral processes but these do not extend posteriorly beyond the fork of the telson; the telsonal furcae bear 1 dorsal and 2 lateral spines each. These differences are not apparent in later zoeal stages, but their presence in the first zoeal stage and the differences noted in the megalopa stage may be reason to question the synonymy of these 2 species.

Xanthid larvae are known to be variable, and it is often difficult to reconcile larval and adult groupings based on morphology. Larvae of some morphologically disparate (as adult) species are very similar, whereas zoeal stages for species in some genera differ markedly in their morphology (see Martin 1984; Martin et al. 1984, 1985; Martin and Abele 1986). Because of the known morphological variability of xanthid larvae, characters presented for taxonomic purposes here and elsewhere (e.g., Martin 1984) must be used with caution.

It is not our intent to promote descriptions of single stages in the life cycles of brachyuran crabs. However, in those cases where a description of a single stage adds appreciably to our knowledge of phylogeny (e.g., Rice 1981b) or fills a gap in the larval biology of a commercially important species complex (present study), we feel such a description is justified. A detailed comparison of zoeal stages of the two species is planned for the near future.

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LITERATURE CITED

FELDER, D. L.
1973. An annotated key to crabs and lobsters (Decapoda, Reptantia) from coastal waters of the northwestern Gulf of Mexico. La. State Univ. Cent. Wetland Resour., Publ. LSU-SG-73-02. Baton Rouge, LA.

FELDER, D. L., J. W. MARTIN, AND J. W. GOY.
1985. Patterns in early postlarval development of decapods. *In* A. M. Wenner (editor), Larval growth, p. 163–225. Crustacean Issues, vol. 2. Balkema Press, Rotterdam.

FELGENHAUER, B. E.
1987. Techniques for preparing crustaceans for scanning electron microscopy. J. Crustacean Biol. 7:71–76.

HYMAN, O. W.
1925. Studies on the larvae of crabs of the family Xanthidae. Proc. U.S. Natl. Mus. 67:1–22.

KAKATI, V. S.
1977. Larval development of the crab, *Menippe rumphii* (Fabricious), as observed in the laboratory (Crustacea, Brachyura). Proc. Symp. Warm Water Zooplankton, UNESCO/NIO Spec. Publ., p. 634–641.

MARTIN, J. W.
1984. Notes and bibliography on the larvae of xanthid crabs, with a key to the known xanthid zoeas of the western Atlantic and Gulf of Mexico. Bull. Mar. Sci. 34:220–239.
In press. Phylogenetic significance of the brachyuran megalopa: evidence from the Xanthidae. *In* A. A. Fincham and P. S. Rainbow (editors), Aspects of decapod crustacean biology. Symp. Zool. Soc. Lond., Vol. 59.

MARTIN, J. W., AND L. G. ABELE.
1986. Notes on male pleopod morphology in the brachyuran crab family Panopeidae Ortmann, 1893, sensu Guinot (1978) (Decapoda). Crustaceana 50:182–198.

MARTIN, J. W., D. L. FELDER, AND F. M. TRUESDALE.
1984. A comparative study of morphology and ontogeny in juvenile stages of four western Atlantic xanthoid crabs (Crustacea: Decapoda: Brachyura). Philos. Trans. R. Soc. Lond., Ser. B, 303:537–604.

MARTIN, J. W., F. M. TRUESDALE, AND D. L. FELDER.
1985. Larval development of *Panopeus bermudensis* Rathbun, 1891 (Brachyura, Xanthidae) with notes on zoeal characters in xanthid crabs. J. Crustacean Biol. 5:84–105.

MONOD, TH.
1956. Hippidea et Brachyura ouest-africains. Mém. Inst. Fr. Afr. Noire 45:1–674.

PORTER, H. J.
1960. Zoeal stages of the stone crab, *Menippe mercenaria* Say. Chesapeake Sci. 1:168–177.

RATHBUN, M. J.
1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae. U.S. Natl. Mus. Bull. 152:1–609.

RICE, A. L.
1981a. The megalopa stage in brachyuran crabs. The Podotremata Guinot. J. Nat. Hist. 15:1003–1011.
1981b. The zoea of *Acanthodromia erinacea* A. Milne Edwards; the first description of a dynomenid larva (Decapoda, Dromioidea). J. Crustacean Biol. 1:174–176.
In press. The megalopa stage in majid crabs, with a review of spider crab relationships based on larval characters. *In* A. A. Fincham and P. S. Rainbow (editors), Aspects of decapod crustacean biology. Symp. Zool. Soc. Lond., Vol. 59.

SCOTTO, L. E.
1979. Larval development of the Cuban stone crab, *Menippe nodifrons* (Brachyura, Xanthidae) under laboratory conditions with notes on the status of the family Menippidae. Fish. Bull., U.S. 77:359–386.

WILLIAMS, A. B.
1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithson. Inst. Press, 550 p.

WILLIAMS, A. B., AND D. L. FELDER.
1986. Analysis of stone crabs: *Menippe mercenaria* (Say), restricted, and a previously unrecognized species described (Decapoda: Xanthidae). Proc. Biol. Soc. Wash. 99:517–543.

OCEANOGRAPHIC ASSOCIATIONS OF NEUSTONIC LARVAL AND JUVENILE FISHES AND DUNGENESS CRAB MEGALOPAE OFF OREGON

JONATHAN M. SHENKER[1]

ABSTRACT

The larval and juvenile fishes and crabs inhabiting the neustonic zone within 50 km of the coast were sampled biweekly from April through July 1984, with a Manta net (mouth 1.0 m wide × 0.7 m deep), and a large neuston trawl (mouth 3.5 m wide × 1.0 m deep). The Manta net was an efficient sampler for larval fishes and crabs, while the neuston trawl collected larger juvenile fishes that had rarely been observed in previous studies.

Nocturnal sampling accounted for nearly all the ichthyoneuston and zooplankton taken. Dungeness crab megalopae were the most abundant species. Although present throughout the survey, the great majority were found in very large aggregations along visible convergence zones or in association with *Velella velella*. Discrete groups of abundant larval and juvenile fishes were found prior to upwelling (*Parophrys vetulus*, *Scorpaenichthys marmoratus*, *Hemilepidotus spinosus*, *Hexagrammos* sp., and *Anoplopoma fimbria*) and after its onset (*Engraulis mordax* and *Sebastes* spp.). These species had distinct zonal (east-west) distribution patterns and were generally associated with, or affected by, hydrographic characteristics such as convergences, upwelling, and the Columbia River plume.

Recent studies of the ichthyoplankton off the northwest coast of the United States have contributed new information on the temporal and spatial occurrences of larvae of coastal and pelagic fish species (Richardson 1973; Richardson and Pearcy 1977; Laroche and Richardson 1979; Richardson et al. 1980; Kendall and Clark 1982a, b; Clark 1984; Bates 1984; Mundy 1983; Brodeur et al. 1985; Boehlert et al. 1985). These surveys focused on larvae occurring below the surface layer of the ocean, although concurrent neustonic samples were occasionally collected (Kendall and Clark 1982 a, b; Clark 1984; Bates 1984; Richardson[2]). Comparison of simultaneous surface and subsurface samples demonstrated that many species were found in both depth strata, while an additional group of species was collected only from the neustonic zone. Brodeur et al. (1987) examined the larval fish and invertebrate components of the neuston in the northeast Pacific, and determined that these organisms were frequent prey items of juvenile salmonids.

Standard plankton and neuston nets used in these studies were effective in collecting the relatively slow-moving early larvae. However, net avoidance by larger larvae and juvenile stages (Barkley 1972; Murphy and Clutter 1972) suggests that use of traditional collecting gear is inappropriate for more mobile fishes. This paper describes the results of a neustonic survey conducted off the Oregon coast in the spring and summer of 1984 that focused on the larger ichthyoneuston. Conventional sampling gear and a new net designed specifically for sampling juvenile fishes were used to characterize the temporal and spatial distribution patterns of both larval and juvenile ichthyoneuston and Dungeness crab, *Cancer magister*, megalopae.

MATERIALS AND METHODS

Sampling was conducted at approximately 2-wk intervals from early April through July 1984, on an east-west transect along the 44°40′N parallel, 3 km north of Newport, OR (Fig. 1). Stations were located at distances of 1, 5, 10, 15, 20, 30, 40, and 50 km from shore. The stations were occupied twice during each 24-h cruise, once during the day and once at night. On one cruise (8–10 June), the 50 km station was occupied for 27 hours to assess diel variation in abundance of neustonic organisms. In response to several

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[2]Richardson, S. L. Oregon's coastal ichthyoneuston - a preliminary report. Unpubl. rep. Presented at American Society of Ichthyologists and Herpetologists, Williamsburg, VA, June 1975.

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FISHERY BULLETIN: VOL. 86, NO. 2, 1988.

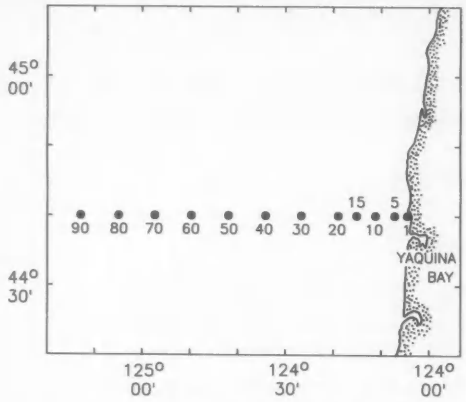

FIGURE 1.—Location of stations along the transect off Newport, OR. The numbers indicate distance offshore in kilometers.

weeks of strong upwelling, during which very few larvae were collected close to the coast, the sampling scheme was modified for the two July cruises by eliminating some of the inshore stations and extending the transect as far offshore as 90 km. Only night samples were collected during July.

One of the primary considerations of the survey was to collect samples while minimizing net avoidance by the target organisms. Reduction of vessel-induced disturbance was accomplished by deploying the collecting gear from the ends of 12 m-long outriggers on the FV *Cumberland Trail*, a chartered 23 m commercial scallop-fishing vessel.

Two different nets were used to collect the samples. Larval fish and zooplankton were collected with a Manta neuston net (Brown and Cheng 1981), modified to have a mouth 1.0 m wide × 0.7 m deep. The Manta frame was equipped with a green-colored 0.333 mm mesh net, PVC cod end bucket, and General Oceanics model 2030 digital flowmeter[3]. A two-point bridle was attached to the upper corners of the frame. Drag on the net while towing kept the entire bridle and towing wire assembly out of the water.

The second net was designed to collect the larger juvenile fishes that were assumed to avoid the smaller Manta net. The neuston trawl was constructed with a mouth 3.50 m wide × 1.05 m deep (Fig. 2a). The frame consisted of 43 mm (outside diameter) heavy-duty galvanized pipe, with towing points welded at the four corners. Flotation for the frame was provided by three inflatable spar buoy floats. These 40 cm diameter floats had hollow tubes running through their centers and were fitted onto the upper bar of the frame. The 8.5 m-long net was made of 4.8 mm green-colored woven mesh, with a 15 cm-wide cloth collar around the mouth, PVC cod end bucket and General Oceanics model 2030 flowmeter. The net had a mouth slightly larger than the frame (3.70 m × 1.20 m) so the net could be laced around the outside of the frame and flotation buoys. The ends of six 12 mm polypropylene rope riblines running the length of the net were shackeled to the frame for additional support. A 4-point bridle of 6.4 mm wire was attached to the corners of the neuston trawl (Fig. 2b). Drag forces kept the entire bridle and towing wire (except for the two short segments attached to the bottom of the frame) out of the water. A length of 5 cm polypropylene rope was attached between the upper towing points on the frame, as a bridle for use in deploying and retrieving the net. A line attached to the retrieval bridle was passed to a hydraulic capstan through a block tied in the rigging over the deck. During a tow, this retrieval line was slackened, but remained attached to the vessel, and floated in a broad arc behind the net mouth.

At each station, the neuston trawl and Manta net were towed simultaneously from the port and starboard outriggers, at approximately 1–1.5 m/second. Tows were generally made either against or with the direction of the prevailing swells. The Manta net was usually fished for approximately 8–9 minutes/tow and filtered about 300–400 m^3. The neuston trawl generally filtered 2,000–3,000 m^3 during a 10–11 minute tow. Additional tows with the neuston trawl were frequently made at a station to assess small-scale patchiness and to sample visible "structures" in the surface layer, such as convergence zones marked by foam lines and rafts of the pleustonic hydroid *Velella velella*.

On several cruises, onset of high winds and rough sea conditions prevented use of the Manta net during the daytime sampling of the transect as we returned toward shore. However, we were able to fish the neuston trawl in winds up to an estimated 40–45 km/hour, and in white-capped seas of 2–3 m. Neuston trawl samples were collected at alternate stations during the periods of adverse weather.

[3]References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

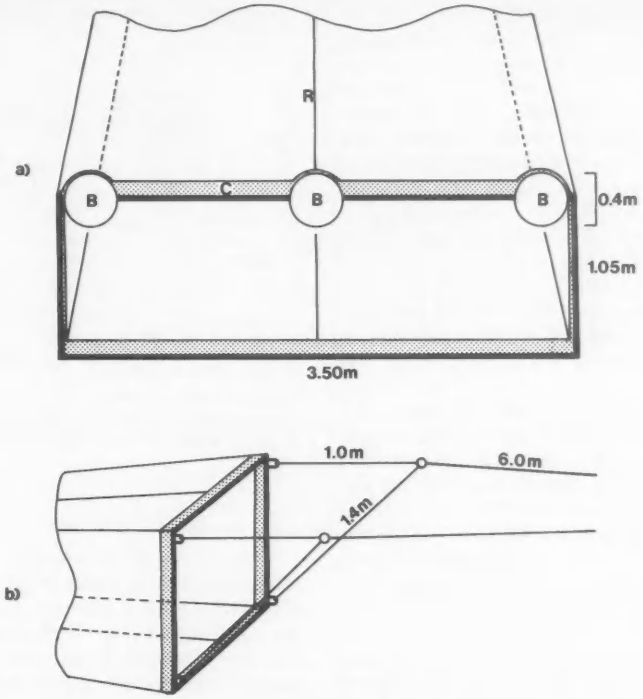

FIGURE 2a.—Front view of the neuston trawl; B = inflated 40 cm diameter spar buoys; C = cloth collar around mouth of net; R = polypropylene rib lines.
FIGURE 2b.—Side view of the neuston trawl showing construction of the towing bridle. Floats were removed for clarity.

Several very large catches of Dungeness crab megalopae in the neuston trawl were subsampled by volume, with the majority of the megalopae being returned alive to the ocean. Samples from both nets were preserved in 10% formalin/seawater and sent to the laboratory for analysis. All larval and juvenile fishes were identified to the lowest practical taxonomic level. After extrapolating catch sizes from subsample counts, the data were normalized to produce density estimates of organisms/1,000 m^3. As an indicator of patchiness of abundant taxa, the coefficient of dispersion (C.D. = $S^2/\overline{X}$) was calculated for the samples in which each taxon was present.

Hydrographic and meteorological data were collected at each station. Surface water temperature was determined with a handheld bucket thermometer. Water samples were collected for laboratory analysis of surface salinity using a Model 8400 Guildline Autosalinometer. A 200 mL surface water sample was filtered through a 0.3 μm pore size Gelman A/E glass fiber filter for determination of chlorophyll a concentration. The filters were stored in dessicant over dry ice at sea, and then in a freezer, before acetone extraction of the chlorophyll a and analysis with a Turner Designs Model 10 Fluorometer. During the daytime, Secchi depths were estimated, using a 30 cm disc, and surface irradiance was measured with a handheld General Electric Model 214 Light Meter. Other data collected included weather and sea state conditions at each station.

RESULTS

Hydrographic Data

The neustonic realm was characterized by distinct temporal and spatial patterns that reflect the highly dynamic springtime oceanographic

processes of the Oregon coastal zone. Daily upwelling indices derived from barometric pressure data (Fig. 3; A. Bakun[4]) indicated that in April and May, local winds varied in direction and strength, with one extended period of stormy weather with southwest winds (negative index values). Temperature and salinity profiles during these months showed relatively little variation along the transect within a sampling period (Fig. 4a, b, c). Chlorophyll a peaks and low salinity near shore may have been due to the influence of water exiting Yaquina Bay. The highest chlorophyll a values were observed following periods of northwest winds, and the highest temperatures occurred after a period of very light winds and high insolation.

The hydrographic regime was altered by the onset of northwest winds in June (Fig. 3), which induced the upwelling of cold, more saline nutrient-rich water along the coast. Strong upwelling [defined by Small and Menzies (1981) as a daily index value >50] was sporadic in June but nearly continuous in July. Temperature, salinity, and chlorophyll a profiles rapidly changed in response to the upwelling-favorable winds (Fig. 5a, b, c).

During the 8–10 June cruise, low temperature and high salinity water was found within 5 km of the coast. Low salinity, warm water more than 15 km offshore apparently was the plume of the Columbia River. By 19–20 June, continued offshore transport of the surface layer pushed the inshore edge of the plume to 40 km off the coast. Low chlorophyll a concentrations, low temperatures, and high salinity near shore on 19–20 June indicated the occurrence of active upwelling.

Upwelling persisted through the end of July. Temperature and salinity profiles were similar to those observed during the second June cruise, with the patterns of increasing temperature and decreasing salinity farther offshore continuing to the limits of sampling of 90 km on 8 and 9 July and to 70 km on 23 and 24 July. During the upwelling in July, a dramatic phytoplankton bloom occurred in the surface waters within 30 km of the coast. Chlorophyll a concentrations here were denser and broader in offshore extent than the surface and subsurface biomass concentrations previously observed off Oregon (Small and Menzies, 1981).

[4]A. Bakun, Pacific Environmental Group, National Marine Fisheries Service, Monterey, CA 93940, pers. commun. August 1984.

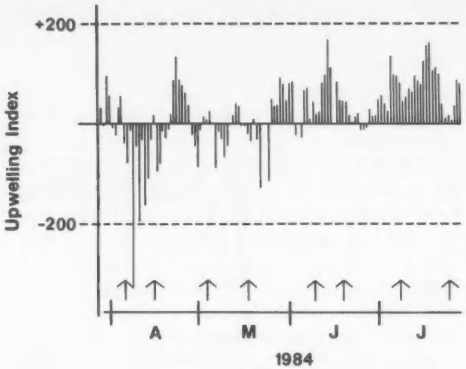

FIGURE 3.—Daily upwelling indices for spring-summer 1984. Positive values >50 indicate occurrence of winds inducing strong upwelling. Arrows indicate dates of sampling cruises.

Ichthyoneuston

A total of 107 Manta net and 142 neuston trawl samples collected 48 taxa of larval, juvenile, and adult fishes. Larvae ≤10 mm and a few juveniles were collected by the Manta net, while large numbers of juvenile fishes up to 60–70 mm were taken by the neuston trawl. Size-frequency data for three of the commonest species (Fig. 6 a, b, c) illustrate the relative ability of the nets to capture different sizes of fishes.

Nighttime sampling (59% of the Manta net tows and 62% of the neuston trawl tows) accounted for 93.3% of all fishes in the Manta net catch and 96.5% of the fishes taken in the neuston trawl (Table 1). Four Manta net and 8 neuston trawl tows made during twilight collected 5.4% and 2.9%, respectively, of the total number of fishes taken with each gear type (Table 2). Only 1.3% of the Manta net catch and 0.6% of the neuston trawl catch was made during daytime (Table 2).

Only two species were not collected predominantly at night. Larval Pacific saury, *Cololabis saira*, were taken in both day and night Manta net samples. Larval northern lampfish, *Stenobrachius leucopsarus*, were abundant only in the twilight samples from early June (Tables 1, 2).

Arbitrary criteria on frequency of occurrence (in >15% of the night samples of either net) or abundance (peak densities >40/1,000 m^3) indicated that nine taxa of larval, juvenile, and adult fishes were dominant components of the ichthyoneuston. Most taxa were characterized by dis-

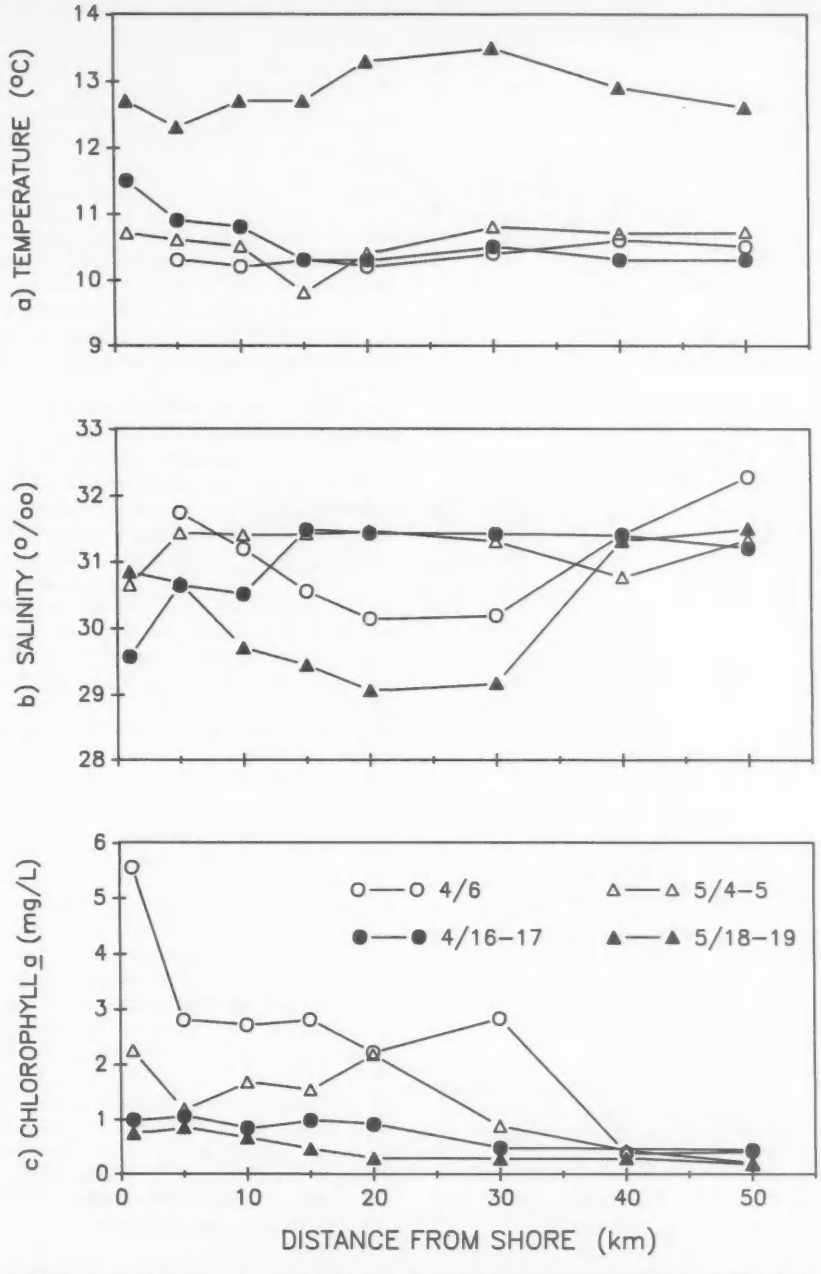

FIGURE 4a-c.—Nighttime environmental conditions observed on each cruise during the pre-upwelling period. a = temperature; b = salinity; c = chlorophyll *a* concentration.

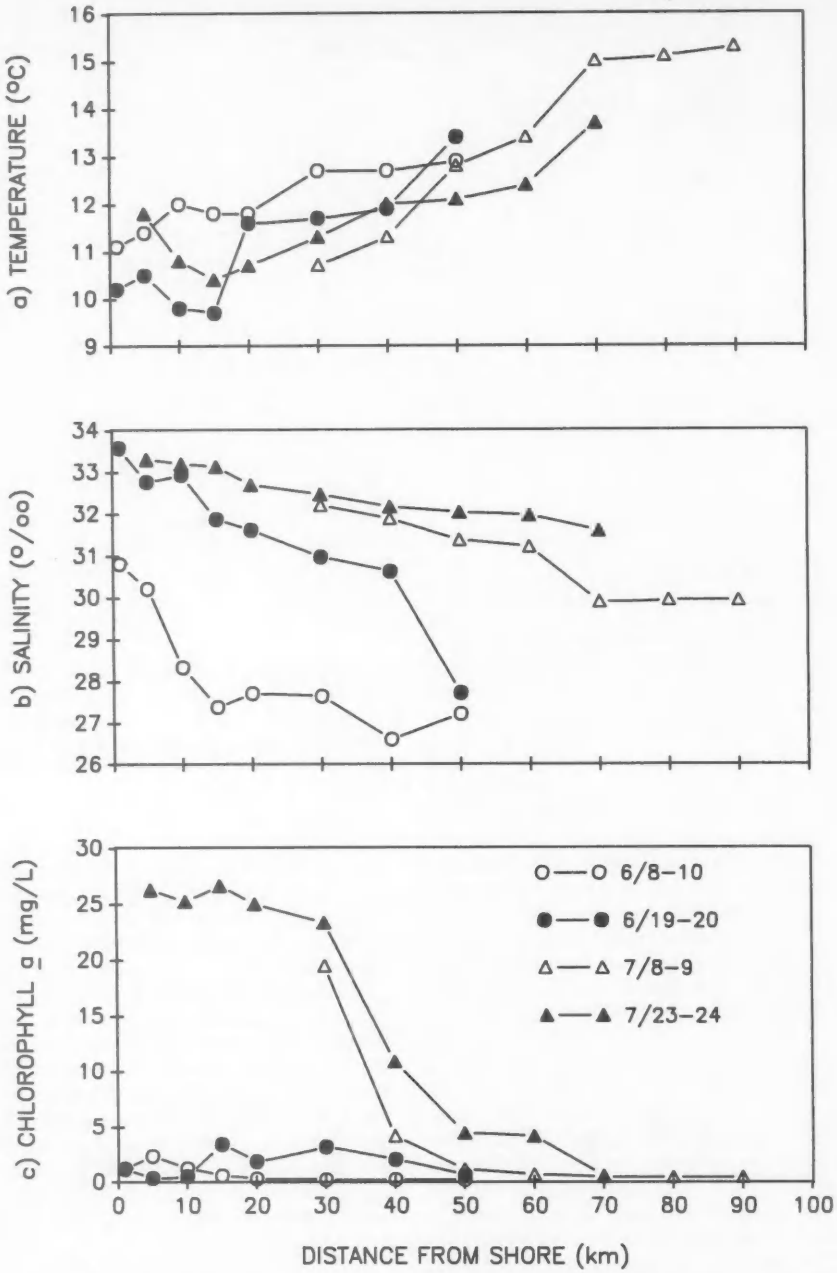

FIGURE 5a-c.—Nighttime environmental conditions observed on each cruise during the upwelling period. a = temperature; b = salinity; c = chlorophyll *a* concentration.

tinct temporal shifts in occurrence: Five taxa were abundant only prior to the onset of continuous upwelling in mid-June, three taxa were sporadically abundant following the beginning of upwelling, and one species (*Ronquilus jordani*) was present throughout the survey.

Pre-upwelling Species

The numerically dominant species in the nearshore region in spring was larval English sole, *Parophyrys vetulus*. These larvae were patchily distributed (C.D. = 32.5) within 30 km offshore, reaching densities of 75/1,000 m^3 in Manta net collections. Larval abundance declined rapidly after April (Table 1). Size-frequency distributions indicated that the Manta net was more effective than the neuston trawl for collecting fish ≤15 mm (Kolmogorov-Smirnov test, $P < 0.01$). Eye migration in the larger fish (20–24 mm) was nearly complete, indicative of their impending shift to a benthic existence. Similar-sized juveniles were taken nearshore in April in benthic tows (B. Mundy[5]).

Cabezon, *Scorpaenichthys marmoratus*, larvae were most abundant in Manta catches in the spring (Table 1), although newly hatched larvae were collected near shore through June. The smallest larvae (4–6 mm) were taken only at the 1–15 km stations, while larvae up to 10 mm were found along the entire transect. These larvae were patchily distributed, with April densities reaching 207/1,000 m^3 (C.D. = 92.7). Frequency of occurrence and larval density declined through early July. Large juvenile cabezon (26–38 mm) were collected by the neuston trawl (Fig. 6a). These juveniles were encountered all along the transect from April to mid-June.

Two dominant taxa found at all stations prior to upwelling were greenling (*Hexagrammos* sp.) and brown Irish lord, *Hemilepidotus spinosus*. Juvenile greenlings were the most frequently collected species, occurring in 44.8% of the nighttime neuston trawl samples (Table 1), although they were rarely taken by the Manta net (Fig. 6b). They were the most evenly dispersed of the abundant fish collected (C.D. = 2.2), and never exceeded densities of 10/1,000 m^3. The two largest catches of greenling were made in association with distinct hydrographic features. Nineteen juveniles were collected from a convergence zone near shore in mid-May (along with 150,000 Dungeness crab megalopae) and 20 juveniles were taken from Columbia River plume water 50 km offshore in early June. Mean lengths of greenling from the neuston trawl samples increased from

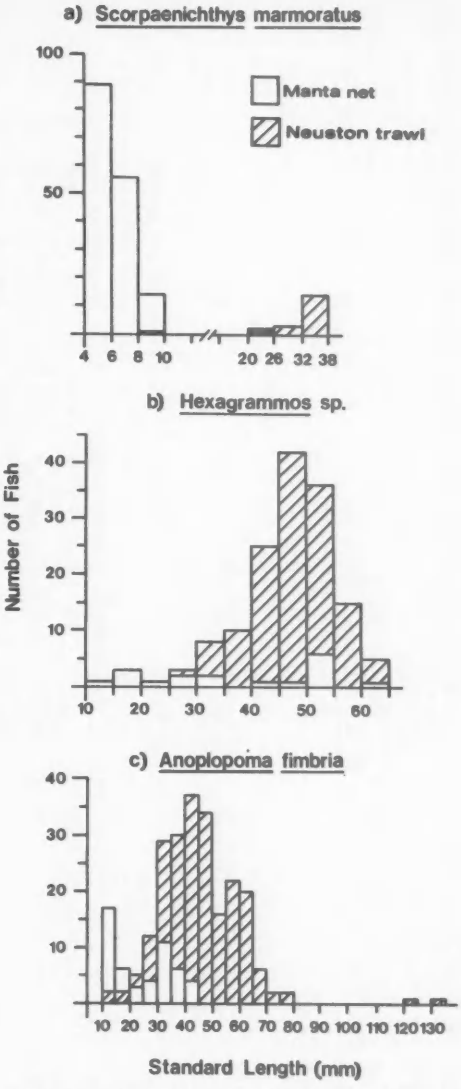

FIGURE 6a-c.—Length-frequency data of larval and juvenile fishes collected by each net. a = *Scorpaenichthys marmoratus*; b = *Hexagrammos* sp.; c = *Anoplopoma fimbria*.

[5]B. C. Mundy, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822, pers. commun. May 1984.

TABLE 1.—Nighttime abundance (A = mean of all catches/1,000 m^3) and frequency of occurre
of the sur

Species	April				May			
	Manta		Trawl		Manta		Trawl	
	A	F(15)	A	F(23)	A	F(16)	A	F(22)
Clupeidae								
Clupea harengus	3.67	2	—	—	—	—	—	—
Engraulidae								
Engraulis mordax	—	—	—	—	—	—	—	—
Salmonidae								
Oncorhynchus keta	—	—	—	—	—	—	0.51	1
O. kisutch	—	—	—	—	—	—	0.73	2
Salmo gairdneri	2.59	1	—	—	—	—	0.60	2
Osmeridae								
unidentified	8.78	2	0.40	1	—	—	0.37	1
Sternoptychidae								
Danaphos oculata	—	—	—	—	—	—	—	—
Myctophidae								
Diaphus theta	—	—	—	—	—	—	—	—
Stenobrachius leucopsarus	—	—	0.43	1	2.36	1	—	—
Symbolophorus californianus	—	—	—	—	—	—	—	—
Tarletonbeania crenularis	—	—	—	—	—	—	0.43	1
Gadidae								
Microgadus proximus	—	—	—	—	—	—	—	—
Scomberesocidae								
Cololabis saira	2.76	3	0.36	2	—	—	0.43	1
Gasterosteidae								
Gasterosteus aculeatus	—	—	—	—	—	—	0.32	1
Bathymasteridae								
Ronquilus jordani	4.50	5	—	—	5.59	6	—	—
Cryptacanthodidae								
Delolepis gigantea	2.63	1	—	—	—	—	—	—
Lyconectes aleutensis	5.00	1	—	—	—	—	—	—
Ammodytidae								
Ammodytes hexapterus	2.58	4	—	—	9.71	1	—	—
Stromateidae								
Icichthys lockingtoni	—	—	—	—	—	—	—	—
Scorpaenidae								
Sebastes crameri	—	—	0.44	1	—	—	0.75	3
S. melanops	—	—	—	—	—	—	—	—
S. pinniger	—	—	—	—	—	—	0.38	1
S. reedi	—	—	—	—	—	—	—	—
Sebastes spp. larvae	19.42	4	—	—	10.42	4	—	—
Sebastes spp. juveniles	—	—	0.43	2	8.99	4	1.62	6
Anoplopomatidae								
Anoplopoma fimbria	3.09	4	1.35	4	10.35	6	3.18	3
Hexagrammidae								
Hexagrammos sp.	3.85	4	0.79	13	3.60	5	1.31	11
Ophiodon elongatus	12.91	2	—	—	6.28	2	—	—
Oxylebius pictus	—	—	0.61	1	—	—	—	—

ccurrence (F = number of catches) of all ichthyoneuston taxa collected by each net during each month he survey in 1984.

	June				July				Total			
awl	Manta		Trawl		Manta		Trawl		Manta		Trawl	
F(22)	A	F(19)	A	F(24)	A	F(15)	A	F(18)	A	F(65)	A	F(87)
—	—	—	—	—	—	—	—	—	3.67	2	—	—
—	1.98	1	0.25	1	127.90	5	0.28	1	106.91	6	0.27	2
1	—	—	—	—	—	—	—	—	—	—	0.51	1
2	—	—	—	—	—	—	0.41	3	—	—	0.54	5
2	—	—	—	—	—	—	—	—	2.59	1	0.60	2
1	—	—	—	—	4.32	2	—	—	6.55	4	0.39	2
—	—	—	—	—	1.68	1	—	—	1.68	1	—	—
—	—	—	—	—	—	—	0.71	1	—	—	0.71	1
—	2.16	1	—	—	2.82	2	—	—	2.54	4	0.43	1
—	—	—	—	—	1.81	1	0.52	3	1.81	1	0.52	3
1	6.28	1	0.38	1	153.11	5	42.71	5	128.64	6	30.62	7
—	—	—	1.02	1	—	—	0.42	1	—	—	0.72	2
1	7.27	3	0.34	4	2.33	5	1.30	3	3.79	11	0.64	10
1	—	—	—	—	—	—	1.29	1	—	—	0.81	2
—	4.53	11	—	—	15.54	5	0.33	2	6.80	27	0.33	2
—	—	—	—	—	—	—	—	—	2.63	1	—	—
—	—	—	—	—	—	—	—	—	5.00	1	—	—
—	1.64	1	—	—	—	—	—	—	3.61	6	—	—
—	—	—	—	—	5.36	3	—	—	5.36	3	—	—
3	2.65	2	0.94	9	—	—	—	—	2.65	2	0.86	13
—	—	—	0.42	3	—	—	1.01	1	—	—	0.57	4
1	—	—	0.28	1	—	—	0.53	2	—	—	0.43	4
—	1.74	3	—	—	—	—	0.34	1	1.74	3	0.34	1
—	18.58	8	—	—	238.28	6	—	—	77.07	22	—	—
6	—	—	0.49	7	1.42	2	—	—	6.47	6	0.93	15
3	8.68	5	11.73	7	—	—	0.34	2	7.86	15	5.97	16
11	1.83	4	1.80	15	—	—	—	—	3.07	13	1.33	39
—	—	—	—	—	—	—	—	—	9.59	4	—	—
—	1.64	1	0.52	1	1.61	1	0.30	1	1.63	2	0.48	3

TABLE 1.—*Continued*.

Species	April				May			
	Manta		Trawl		Manta		Trawl	
	A	F(15)	A	F(23)	A	F(16)	A	F(22)
Cottidae								
Artedius harringtoni	3.44	3	—	—	9.71	1	0.36	1
Cottus asper	15.68	2	—	—	—	—	—	—
Hemilepidotus spinosus	5.45	3	1.05	12	7.39	7	6.11	15
Leptocottus armatus	19.09	1	—	—	2.22	1	—	—
Scorpaenichthys marmoratus	47.19	10	0.47	5	15.16	5	0.37	3
Agonidae								
Agonopsis vulsa	—	—	0.37	1	—	—	0.45	2
Liparididae								
unidentified	3.99	2	1.28	1	—	—	—	—
Bothidae								
Citharichthys sordidus	—	—	0.41	1	—	—	—	—
C. stigmaeus	—	—	0.43	4	—	—	0.67	2
Pleuronectidae								
Eopsetta jordani	—	—	—	—	—	—	0.39	2
Glyptocephalus zachirus	2.50	1	—	—	—	—	—	—
Isopsetta isolepis	—	—	0.41	1	—	—	—	—
Parophrys vetulus	22.38	6	4.42	9	2.53	3	0.68	5
Pleuronichthys sp.	—	—	—	—	—	—	—	—
Psettichthys melanostictus	9.48	3	—	—	—	—	—	—
Unidentifiable	7.92	4	—	—	—	—	0.51	1
Total number of taxa	22		16		13		20	
Mean abundance/1,000 m^3	63.53		3.39		22.68		6.43	

	June				July				Total			
awl	Manta		Trawl		Manta		Trawl		Manta		Trawl	
F(22)	A	F(19)	A	F(24)	A	F(15)	A	F(18)	A	F(65)	A	F(87)
1	4.51	3	—	—	1.74	1	—	—	4.39	8	0.36	1
—	4.47	2	—	—	—	—	—	—	10.07	4	—	—
15	2.40	3	3.77	6	—	—	—	—	5.79	13	3.84	33
—	—	—	—	—	—	—	—	—	10.66	2	—	—
3	3.11	10	0.76	5	2.66	2	—	—	21.63	27	0.56	13
2	—	—	0.46	4	—	—	0.34	2	—	—	0.42	9
—	2.91	6	0.57	7	3.85	4	0.34	3	3.39	12	0.57	11
—	—	—	—	—	—	—	—	—	—	—	0.41	1
2	1.98	1	1.24	7	—	—	0.50	4	1.98	1	0.81	17
2	—	—	0.71	2	—	—	—	—	—	—	0.55	4
—	—	—	—	—	—	—	—	—	2.50	1	—	—
—	—	—	—	—	—	—	—	—	—	—	0.41	1
5	1.59	1	0.25	1	—	—	—	—	14.35	10	2.89	15
—	—	—	0.51	1	—	—	—	—	—	—	0.51	1
—	8.04	1	6.61	2	2.20	1	—	—	7.74	5	6.61	2
1	2.32	3	—	—	3.89	3	—	—	5.29	10	0.51	1
0	21		20		17		17		33		34	
43	20.64		7.48		199.91		12.81		72.49		7.24	

TABLE 2.—Daytime abundance (A = mean of all catches/1,000 m^3) and frequency of occurrence
3 months of the survey. Daytime samples were not collected in July. Twilight sampling (45 minut
1984.

	April				May			
	Manta		Trawl		Manta		Trawl	
Species	A	F(15)	A	F(17)	A	F(8)	A	F(12)
Engraulidae								
Engraulis mordax	—	—	—	—	—	—	—	—
Osmeridae								
unidentified	—	—	—	—	—	—	—	—
Myctophidae								
Stenobrachius leucopsarus	—	—	—	—	—	—	—	—
Scomberesocidae								
Cololabis saira	2.48	4	—	—	—	—	—	—
Bathymasteridae								
Ronquilus jordani	—	—	—	—	—	—	—	—
Cryptacanthodidae								
Lyconectes aleutensis	2.54	1	—	—	—	—	—	—
Ammodytidae								
Ammodytes hexapterus	—	—	—	—	—	—	—	—
Scorpaenidae								
Sebastes crameri	—	—	—	—	—	—	0.32	1
S. mystinus	—	—	—	—	—	—	—	—
Sebastes spp. larvae	—	—	—	—	—	—	—	—
Sebastes spp. juveniles	—	—	—	—	—	—	—	—
Anoplopomatidae								
Anoplopoma fimbria	2.60	1	—	—	2.87	1	0.38	1
Hexagrammidae								
Hexagrammos sp.	2.74	2	0.81	2	—	—	—	—
Ophiodon elongatus	2.52	2	—	—	—	—	—	—
Cottidae								
unidentified	—	—	—	—	1.57	2	—	—
Clinocottus globiceps	—	—	—	—	—	—	—	—
Hemilepidotus spinosus	—	—	—	—	—	—	0.35	1
Scorpaenichthys marmoratus	2.52	2	—	—	—	—	—	—
Liparididae								
unidentified	—	—	—	—	—	—	—	—
Pleuronectidae								
Eopsetta jordani	—	—	—	—	—	—	—	—
Parophrys vetulus	2.76	1	0.94	1	—	—	0.32	1
Unidentifiable	—	—	—	—	—	—	—	—
Total number of taxa	7		2		2		4	
Mean abundance/1,000 m^3	2.22		0.15		0.75		0.11	

urrence (F = number of samples) of all ichthyoneuston taxa collected by each net during the first
5 minutes before and after sunset and sunrise) was conducted at the 50 km station on 8-10 June,

	June				Daytime total				June twilight			
	Manta		Trawl		Manta		Trawl		Manta		Trawl	
12)	A	F(13)	A	F(18)	A	F(36)	A	F(47)	A	F(6)	A	F(8)
—	2.41	4	—	—	2.41	4	—	—	—	—	—	—
—	1.56	1	—	—	1.56	1	—	—	—	—	—	—
—	1.89	1	—	—	1.89	1	—	—	27.62	3	—	—
—	2.44	4	—	—	2.46	8	—	—	2.75	3	—	—
—	—	—	—	—	—	—	—	—	4.71	3	—	—
—	—	—	—	—	2.54	1	—	—	—	—	—	—
—	—	—	0.33	1	—	—	0.33	1	—	—	—	—
1	—	—	—	—	—	—	0.32	1	—	—	0.97	2
—	—	—	—	—	—	—	—	—	1.50	1	—	—
—	5.39	2	—	—	5.39	2	—	—	4.59	2	—	—
—	—	—	—	—	—	—	—	—	4.50	1	0.50	2
1	—	—	—	—	2.74	2	0.38	1	2.30	2	1.48	5
—	—	—	—	—	2.74	2	0.81	2	—	—	1.10	3
—	—	—	—	—	2.52	2	—	—	—	—	—	—
—	—	—	—	—	1.57	2	—	—	—	—	—	—
—	1.57	1	—	—	1.57	1	—	—	—	—	—	—
1	—	—	—	—	—	—	0.35	1	10.30	2	1.17	7
—	1.58	1	—	—	2.20	3	—	—	1.93	1	0.46	1
—	—	—	—	—	—	—	—	—	—	—	0.37	1
—	1.61	1	—	—	1.61	1	—	—	—	—	—	—
1	—	—	—	—	2.76	1	0.63	2	—	—	—	—
—	1.89	2	—	—	1.89	2	—	—	—	—	—	—
	9		1		15		6		9		7	
	3.24		0.02		2.26		0.08		24.60		2.83	

38.8 mm ($N = 10$) in early April to 51.2 mm ($N = 72$) during the first June cruise.

Brown Irish lord juveniles were the numerically most abundant and the second most frequently occurring species (Table 1). Early juveniles (10–20 mm) were taken with both nets in April and May only at the offshore (40–50 km) stations. Larger juveniles (20–30 mm) were patchily distributed from April through mid-June all along the transect (C.D. = 14.1). Although 47% of the total number of trawl caught specimens were taken in densities below 15/1,000 m^3, repeated sampling in one large aggregation accounted for the bulk of the catch. Three sequential tows at the 50 km station on 5 May had juvenile densities of 15–39/1,000 m^3 , but distinctive hydrographic characteristics at the station were not detected.

The only species with a characteristic offshore distribution prior to upwelling was sablefish, *Anoplopoma fimbria*. Small juveniles (10–45 mm) were effectively taken by the Manta net, while the neuston trawl was more efficient at collecting 30–70 mm specimens (Fig. 6c). The 10–50 mm fish were collected primarily at the 50 km station from April through mid-June, although several specimens were taken closer inshore. The 50–75 mm fish were captured only on 8–10 June from the Columbia River plume water at the 50 km station. After the onset of upwelling, two individuals (120–130 mm) were taken 80–90 km from shore.

Upwelling Species

Three taxa were abundant on only one of three cruises made after the onset of upwelling in mid-June (Table 1). Distributions of northern anchovy, *Engraulis mordax*, larvae; rockfish (*Sebastes* spp.) larvae; and adult blue lanternfish, *Tarletonbeania crenularis*, overlapped at some offshore stations on 8 and 9 July. The offshore portion of the transect was characterized by a drop in salinity and an increase in temperature between 60 and 70 km offshore (Fig. 5a, b), indicating a transition from coastal to Columbia River plume water.

Of the 814 rockfish larvae collected throughout the survey, 87% were taken at the 50–90 km stations on this cruise, with a peak density of the 3.5–7.0 mm larvae of 684/1,000 m^3. Adult blue lanternfish were present in densities up to 315/1,000 m^3 at the 60–90 km stations. Lanternfish from simultaneous Manta and neuston trawl tows displayed no difference in length-frequency distributions, although a significant change in the size structure of the catches between stations was observed (K-S test, $P < 0.01$). Mean size of the fish decreased approximately 10% between adjacent stations, from 50.9 mm at 60 km to 37.8 mm at 90 km. Anchovy larvae (3–9 mm) were restricted to the lower salinity plume water at the 70–90 km stations, with peak and mean densities of 368 and 210/1,000 m^3, respectively.

Persistant Species

Only northern ronquils, *Ronquilus jordani*, were abundant in both pre-upwelling and upwelling periods. The elongate larvae and juveniles were collected with the Manta net starting in mid-April, with abundances peaking at 40/1,000 m^3 in July. Mean lengths over this time interval increased from 8.7 mm ($n = 8$) to 26.6 mm ($n = 43$). Ronquils were relatively dispersed along the transect (C.D. = 7.6), and size or seasonal patterns of distribution were not detected.

Dungeness Crab Megalopae

Dungeness crab megalopae were the dominant component of the catches throughout the survey, with an estimated total of 350,000 megalopae collected in 249 hauls. The megalopae were found at most stations during all cruises (Fig. 7), although they were rare seaward of 50 km in July. Megalopae were present in 71.4% of the Manta net daytime tows and 93.8% of the nighttime tows, and in 90.9% and 98.9% of the day and night neuston trawl collections, respectively. All twilight hauls captured megalopae.

Despite the higher frequency of occurrence of megalopae in the neuston trawl, the Manta net was a more accurate estimator of their abundance. For 58 pairs of nighttime catches with densities under 2,000/1,000 m^3, the Manta net caught approximately 3 times as many megalopae per m^3 as the neuston trawl. The 4.8 mm mesh of the neuston trawl apparently enabled some megalopae to pass through the mesh, and some escapement was observed while the trawl was sitting on deck after retrieval. More similar estimates between the nets were obtained when higher densities of megalopae were sampled, probably because of clumping of the large (11 mm total length) spiny megalopae into large masses which clogged the mesh.

In general, densities of megalopae caught by

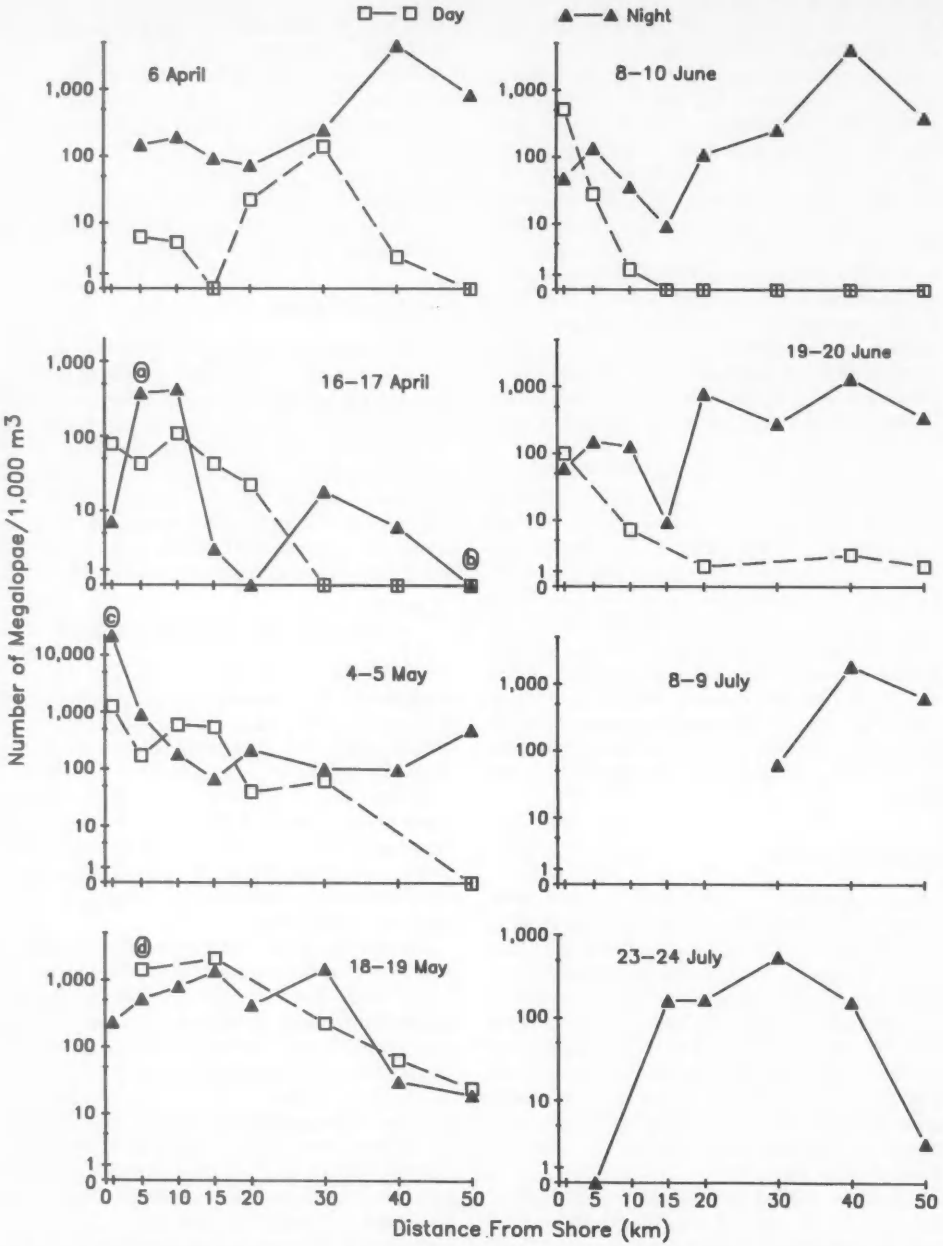

FIGURE 7.—Daytime and nighttime densities of megalopae collected by the Manta net. Rough weather prevented the use of the Manta net during the day of 19 May; neuston trawl data for this portion of the cruise are presented. Circled letters refer to events discussed in the text.

the Manta net in the daytime were lower than at night for each station (Fig. 7). The differences between day and night were particularly apparent on bright sunny days and at the offshore stations. Only one of 13 samples of megalopae collected when light intensity exceeded 4,000 lux had a density over 200/1,000 m^3, while 12 of 24 day samples collected at lower light levels exceeded this density. Highest daytime densities (1,600–2,400/1,000 m^3 in neuston trawl samples) were observed on 19 May when a sudden shift in weather before daybreak resulted in very dark, overcast and rainy skies, with 40–45 km/hour winds and 2–3 m breaking waves.

Water clarity may also affect the daytime abundance estimates of megalopae in the neuston along the transect. Daytime densities were always low seaward of 30 km where Secchi depths exceeded 9 m, while higher densities were observed in the more turbid near-coastal waters with Secchi depths of 4–9 m.

The 27-h occupancy of the 50 km station on 8–9 June provided additional evidence of a distinct diel pattern in utilization of the neustonic habitat by megalopae (Fig. 8). Abundance of megalopae peaked during the twilight periods of dawn and dusk. A significant decrease in abundance was noted in the middle of the night, while midday samples did not collect any megalopae.

In addition to the wide distribution of megalopae along the transect, sampling occasionally detected the aggregation of very large numbers of megalopae (denoted by letters over station blocks in Figure 7). These aggregations were typically associated with hydrodynamic or biological structures in the surface layer.

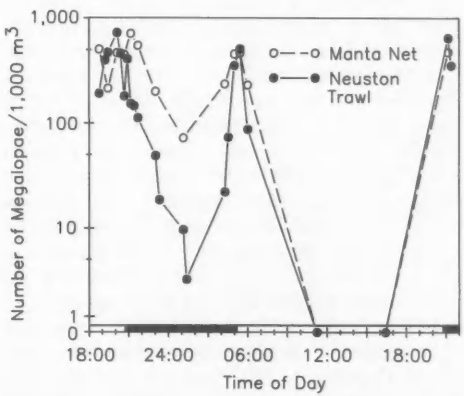

FIGURE 8.—Density of megalopae collected by both nets during a 27 h sampling period 50 km offshore on 8–9 June.

Event A: Simultaneous tows with the Manta net and neuston trawl caught megalopae in densities of 373 and 325/1,000 m^3. The neuston trawl was then redeployed and towed along a foam line marking a surface convergence. An estimated 60,000 megalopae were collected from the convergence zone (24,000/1,000 m^3).

Event B: A series of five consecutive tows with the trawl net was made. Each tow covered a linear distance of approximately 1 km in a westward direction, with an estimated distance of 300 m between tows. Megalopae were very sparse in the simultaneous Manta and trawl tows at the beginning of the series, with densities of 0 and 1.9/1,000 m^3, respectively. The subsequent neuston trawl tows produced density estimates of 79, 3,555, 2,414 and 187/1,000 m^3. Apparently, the megalopae were aggregated over an area extending at least 5 km in the east-west direction.

Event C: Following a period of southwest winds, a large raft of *Velella velella* was found around the inshore station. *Velella velella* were generally found at offshore stations but at densities far lower than the 36 kg/1,000 m^2 level taken here. Although the overall extent of the raft could not be determined at night, the density of megalopae was estimated by both nets at 21,500/1,000 m^3.

Event D: The density of megalopae sampled by the Manta net was 790/1,000 m^3, while a simultaneous neuston trawl tow along a convergence zone only 30 m away collected 150,000 megalopae (46,400/1,000 m^3).

Census estimates of megalopal abundance were computed from nighttime samples for each date (Fig. 9). A modification of Smith's regional census estimate (1972) was used to compute the total number of megalopae occurring in a 1 m wide × 1 m deep track along the surface from the coast to 55 km offshore:

$$C_k = \sum_{i=1}^{n} (A_i D_i)$$

where C_k = estimate of abundance of megalopae per meter of coastline during cruise k

A_i = volume of water in the track surrounding station i, computed from

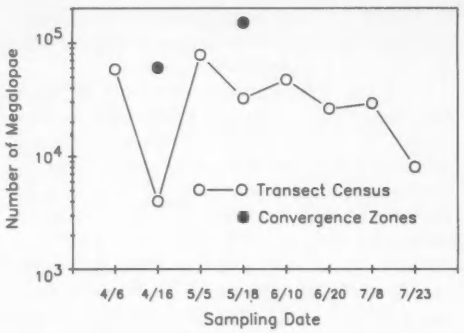

FIGURE 9.—Census estimates of Dungeness crab megalopae at night from Manta net samples for each cruise in a 1 m wide × 1 m deep track extending from the coast to 55 km offshore (30–95 km offshore on 7/8). Single samples from convergence zones sampled with the neuston trawl contained more megalopae than the entire census estimates for the respective cruises.

the midpoints of the distances between the adjacent stations

D_i = density of megalopae at station i.

Although census estimates varied between cruises from approximately 4,000–78,000, these estimates ignored the concentrations of megalopae in convergence zones or other aggregations that were sampled by the neuston trawl. The convergences alone contained 5–15 times more megalopae than the entire census estimates for their respective cruises.

DISCUSSION

The neustonic habitat off Oregon is a dynamic environment that supports an abundant and diverse fauna including Dungeness crab larvae and numerous fish species. The large mouth size of the neuston trawl and minimal disturbance from the vessel probably contributed to larger catches of surface-dwelling ichthyofauna than have been made in previous studies in the same region (Boehlert et al. 1985).

Several species of neustonic organisms were associated with specific oceanographic features such as convergence zones and water masses like the Columbia River plume. These aggregations of Dungeness crab megalopae and several fish species accounted for the major portion of the total catch of each taxon. Recent studies by Shanks (1983, 1985) and Kingsford and Choat (1985, 1986) further emphasize the importance of aggregation of neustonic organisms in oceanic convergences, surface slicks, and around floating objects. This information clearly demonstrates that randomized or grid sampling plans will often fail to detect micro- or meso-scale features of the environment. Surveys may thus severely underestimate the abundance of species, and important data on ecological characteristics such as predator-prey interactions may not be obtained. This is particularly important in understanding the role of spatial co-occurrence of patches of larval fishes and their prey on larval survival and growth (Lasker 1975, 1981; Grover and Olla 1986).

Diel patterns in abundance were striking. Most of the neustonic organisms were collected at night, and their absence from daytime collections may be attributed to vertical migration out of the surface layer or to visual avoidance of the nets. The fact that very few larval or juvenile sablefish and greenlings were collected in subsurface samples in earlier studies (e.g., Richardson and Pearcy 1977; Richardson et al. 1980; Kendall and Clark 1982a; Clark 1984), suggests that these fishes are obligate inhabitants of the neuston, and their low abundance in daytime hauls indicates substantial visual avoidance of the nets.

Conversely, other species may be facultative neuston that undergo diel migrations into the surface layer (Hempel and Weikert 1972), where they can most easily be assessed. Dungeness crab megalopae, in particular, disperse to at least 50 m during the day, but concentrate at the surface at dawn and dusk (Booth et al. 1985). Still other species (the pseudoneuston) may have depth ranges that overlap with the surface layer.

Previous studies on northwest ichthyoplankton have defined basic coastal, transitional, and offshore assemblages of species during different seasons (Richardson and Pearcy 1977; Richardson et al. 1980; Kendall and Clark 1984a, b; Clark 1984). In general, the transitional region roughly parallels the shelf break (approximately 30–40 km offshore in the vicinity of Newport, OR). Richardson et al. (1980) ascribed the consistency of these zonal assemblages to the spawning habits of adults and larval transport in the alongshore coastal circulation. According to Parrish et al. (1981), the spatial and temporal patterns of spawning, and durations of pelagic larval stages of these species, should correspond with the surface drift patterns of the region to minimize larval advection out of suitable habitats. In the Pacific Northwest, species with larvae adapted to the nearshore zone should spawn from fall

through early spring when net surface drift is primarily northward and onshore. Oceanic larvae, however, should be spawned following the spring-summer transition when upwelling results in southward and offshore transport.

The onshore/offshore distributions of several abundant fish species in 1984 were similar to those described earlier, and their seasonal occurrence usually coincided with the constraints discussed by Parrish et al. (1981). However, four species had distributions that crossed the previously described zonal boundaries (Fig. 10). Early cabezon larvae appeared to disperse offshore as they grew. In contrast, early juvenile brown Irish lords were collected offshore in the early spring, while the larger juveniles spread inshore across all stations. Larval greenlings have only been collected close to the coast in late fall (Bates 1984), while the juveniles collected in this study were found at all stations prior to upwelling. Juvenile ronquils were also distributed along the transect, during both non-upwelling and upwelling conditions.

The dispersion of organisms across the transition zone may have been accomplished by several mechanisms. Physical transport of the organisms by mesoscale hydrographic events (e.g., eddies, offshore jets, and meanders in the alongshore currents) (Ikeda and Emery 1984; Mooers and Robinson 1984; Abbott and Zion 1985; Davis 1985) undoubtedly play important roles in the onshore/offshore dispersal of planktonic organisms. Transport with these events may be accelerated or hindered by diel vertical migration into water layers with different zonal flow patterns. Additionally, several species (especially greenling and sablefish) are rapid swimmers whose mobility can contribute to their dispersal or aggregation.

The rapid change in the composition of the ichthyoplankton fauna following the onset of upwelling has not been previously observed. Fishes abundant prior to upwelling may respond to the change in the environment in different ways. The disappearance of greenling and brown Irish lord juveniles suggests upwelling triggered settlement of these fishes to the demersal habitat utilized by older juveniles and adults. A possible stimulus for this transition is the breakdown of the thermocline, which has been identified as a

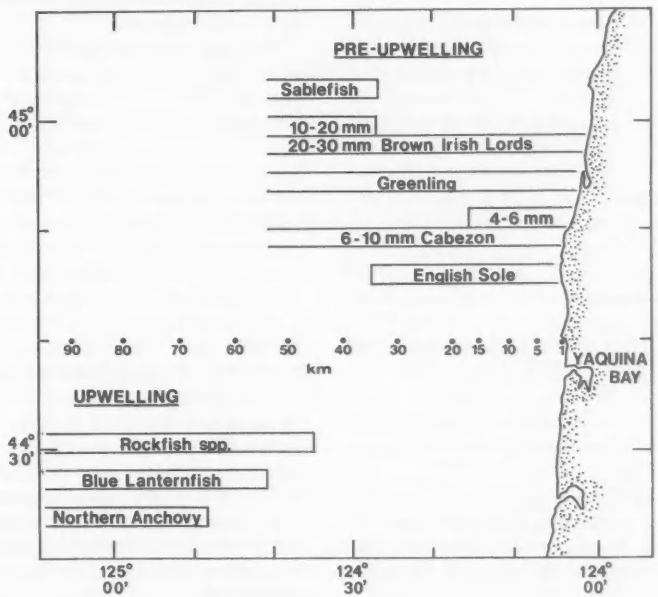

FIGURE 10.—Summary of the zonal distributions of larval and juvenile neustonic fishes in the pre- and early upwelling period (April through mid-June) and the strong upwelling period (July).

barrier to settlement to neustonic juvenile red hake, *Urophycis chuss*, (Steiner et al. 1982; Steiner and Olla 1985).

In contrast, juvenile sablefish apparently remain in the water column off Oregon following the transition to upwelling conditions. Small juveniles (<50 mm) have been captured as far as 250 km offshore in the spring (Kendall and Clark 1982a), and specimens up to 250 mm have been collected from the surface waters in late summer with a purse seine (Brodeur and Pearcy 1986). The very rapid growth rates of young juveniles, reaching 2 mm/day (Boehlert and Yoklavich 1985; Shenker and Olla 1986), undoubtedly resulted in their increasing ability to avoid the towed neuston nets used in this study.

The most abundant larvae occurring after the onset of upwelling were northern anchovy and rockfish. As observed in previous studies (Richardson 1973, 1980; Richardson et al. 1980), these larvae were primarily found offshore. The occurrence of these species, along with a high abundance of vertically migrating blue lanternfish, on the periphery of the Columbia River plume 60–90 km offshore on only one cruise, further illustrates the patchy nature of neustonic distributions.

Although the fish fauna in 1984 was generally characterized by discrete temporal and/or spatial limitations, the occurrence of Dungeness crab megalopae transcended these limits through the 4-mo study. Megalopae were the most abundant organisms collected throughout the survey, but their abundance varied widely between adjacent stations, with occasional very dense patches. Similar patchy distributions of megalopae were observed off British Columbia by Booth et al. (1985), who measured horizontal patch dimensions of 2–4 km. Several dense swarms of megalopae were observed in Bodega Bay, CA, during 1985 (Shenker and Botsford[6]). These patches were long, sinuous aggregations extending 10–20 m along the surface, approximately circular in cross section and about 1 m in diameter. Densities were visually estimated to be on the order of thousands of megalopae per m^3.

The temporal occcurrence of crab larvae in the plankton spans two distinctly different oceanic regimes, and the larvae are potentially transported long distances by the seasonal currents. Larvae typically hatch in mid-winter, pass through 5 zoeal stages in approximately 90 days, and then a month-long megalops stage before settling to the bottom (Reilly 1983a). After hatching, zoeae are released into the northerly flowing Davidson Current. Despite a general onshore component of flow of the Davidson Current, older zoeal stages have been found progressively farther offshore (Lough 1976; Reilly 1983a).

About the time of the spring transition in the alongshore currents from a northerly to southerly direction (Huyer et al. 1975), zoeae metamorphose into megalopae. To survive, these megalopae must be transported back toward the shore, and settle to the bottom in depths shallower than 25 m (Reilly 1983b). Larvae have been found at least 100 km from shore (Lough 1976), although it is unclear if these larvae make it back to shore, or are simply lost from the population.

Again, an apparent anomaly exists between the directions of movement of megalopae and surface waters, where the Ekman layer moves offshore in response to upwelling winds. These discrepancies may be explained by mesoscale mixing processes, as cited earlier. Alternatively, the diel vertical movements of the larvae can move them into different water masses with different directions of zonal movement.

The data from this study and previous research on vertical migration indicate that at least the early zoeal stages and megalopae move to the surface during twilight, and below the surface during the day (Reilly 1983a). Surface abundance estimates of megalopae obtained in the 27-h sampling on 8–9 June (Fig. 8), and by Booth et al. (1985), decreased during the middle of the night. This movement away from the surface is an example of "midnight scattering", perhaps resulting from the lack of a light cue to orient planktonic organisms to the surface (Owen 1981). If midnight scattering is typical for megalopae, abundance estimates made by sampling along a transect throughout the night (Figs. 7, 9) probably underestimate the actual abundance of megalopae utilizing the surface habitat. Megalopae have been collected as deep as 50–70 m during the day (Booth et al. 1985; Shenker and Botsford fn. 6). These observations correlate with Jacoby's (1982) laboratory demonstration that megalopae are positively phototactic to dim light, but avoid bright light.

The present study indicates that the phototactic response of megalopae may assist their return to shore in several ways. Downward movement

[6]Shenker, J. M., and L. W. Botsford, University of California, Bodega Marine Laboratory, P.O. Box 247, Bodega Bay, CA 94923, unpubl. data.

during sunny days, when upwelling wind stress and offshore Ekman transport is generally strongest, can move the larvae into the slow onshore flow below the surface Ekman layer (Peterson et al. 1979). In contrast to the usual northerly upwelling winds, occasional storms blow from the southwest, driving the surface layer onshore. The occurrence of megalopae at the surface during the day was most pronounced on these dark stormy days (especially on the second May cruise), and thus may facilitate their onshore transport.

Observations of megalopae entering into embayments and nearshore areas from Washington to northern California in 1984 and 1985 indicated a dramatic increase in the abundance of megalopae and an extended seasonal occurrence in the plankton, as compared to previous years (Shenker and Botsford fn. 6; Armstrong[7]). This high abundance of crab larvae may presage an upswing in the cyclical crab fishery along these coasts.

Numerous mechanisms have been proposed as causes of the 10-yr cycles in crab abundance. Although some hypotheses have been discounted, several models have survived scrutiny as possible causes of the cycles (see Botsford 1986 for review). Potential mechanisms of environmental forcing of the cycles focus on larval transport and survival. Johnson et al. (1986) detected periodic 10-yr cycles in the occurrence and strength of southward stress during the late larval period that significantly correlated with commercial crab catch 4 and 5 years later. This lag corresponds to the time between larval settlement and growth into the adult fishery (Botsford 1984).

Model simulations by Botsford (1986) indicated that nonlinear effects of wind on larval transport can produce the cyclical swings in crab abundance. However, the models do not preclude the possibility that density-dependent phenomena (such as cannibalism by adult crabs on newly settled juveniles, and predation by nemertean worms on egg masses) may act in concert with the environmental forcing to produce the observed cycles.

The water's surface is the only oceanic habitat that is easily accessible to observation using techniques ranging from satellite and aerial scanning to shipboard visual sighting of targets and continuous monitoring of environmental parameters. Because of this accessibility, micro- and mesoscale patterns in distribution of neustonic taxa and their associations with hydrographic and biological characteristics of the surface zone can be determined more easily than in other environments. The neustonic realm thus offers an excellent opportunity to investigate the mechanisms of transport of the early stages into appropriate nursery habitats, and the availability of food for growth that are required for successful recruitment into adult stocks (Hjort 1914; Lasker 1975, 1981; Frank and Leggett 1982; Sinclair et al. 1984).

[7]D. A. Armstrong, School of Fisheries, WH-10, University of Washington, Seattle, WA 98195, pers. commun. October 1984.

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LITERATURE CITED

ABBOTT, M. R., AND P. M. ZION.
1985. Satellite observations of phytoplankton variability during an upwelling event. Cont. Shelf Res. 4:661–680.

BARKLEY, R. A.
1972. Selectivity of towed net samplers. Fish. Bull., U.S. 70:799–820.

BATES, R. D.
1984. Ichthyoplankton off Washington, Oregon and northern California, October-November, 1981. Natl. Mar. Fish. Serv., Northwest and Alaska Fish. Cent. Process. Rep. 84–12, 41 p.

BOEHLERT, G. W., D. M. GADOMSKI, AND B. C. MUNDY.
1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fish. Bull., U.S. 83:611–622.

BOEHLERT, G. W., AND M. M. YOKLAVICH.
1985. Larval and juvenile growth of sablefish, *Anoplopoma fimbria*, as determined from otolith increments. Fish. Bull., U.S. 83:475–481.

BOOTH, J., A. PHILLIPS, AND G. S. JAMIESON.
1985. Fine scale spatial distribution of *Cancer magister* megalopae and its relevance to sampling methodology. *In* B. R. Melteff (editor), Proceedings of the symposium on Dungeness crab biology and management, p. 273–286. Univ. Alaska Sea Grant Coll. Program, Rep. No. 85-3. Fairbanks, AK 99701.

BOTSFORD, L. W.
1984. Effect of individual growth rate on expected behav-

ior of the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 41:99–107.

1986. Population dynamics of the Dungeness crab (*Cancer magister*). *In* G. S. Jamieson and N. Bourne (editors), North Pacific workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92:140–153.

BRODEUR, R. D., D. M. GADOMSKI, W. G. PEARCY, H. P. BATCHELDER, AND C. B. MILLER.

1985. Abundance and distribution of ichthyoplankton in the upwelling zone off Oregon during anomalous el Niño conditions. Estuarine Coastal Shelf Sci. 21:365–378.

BRODEUR, R. D., B. C. MUNDY, W. G. PEARCY, AND R. W. WISSEMAN.

1987. The neustonic fauna in coastal waters of the northeast Pacific: Abundance, distribution, and utilization by juvenile salmonids. Oreg. State Univ. Sea Grant Coll. Program, Rep. ORESU-T-87-001. Corvallis, OR 97331.

BRODEUR, R. D., AND W. G. PEARCY.

1986. Distribution and relative abundance of pelagic nonsalmonid nekton off Oregon and Washington, 1979–1984. U.S. Dep. Commer., NOAA Tech. Re NMFS 46, 85 p.

BROWN, D. M., AND L. CHENG.

1981. New net for sampling the ocean surface. Mar. Ecol. Prog. Ser. 5:225–227.

CLARK, J. B.

1984. Ichthyoplankton off Washington, Oregon and northern California, May-June, 1981. Natl. Mar. Fish. Serv., Northwest and Alaska Fish. Cent. Process. Rep. 84–11, 46 p.

DAVIS, R. E.

1985. Drifter observations of coastal surface currents during CODE: the method and descriptive view. J. Geophys. Res. 90:4741–4755.

FRANK, W. T., AND W. C. LEGGETT.

1982. Coastal water mass replacement: its effect on zooplankton dynamics and the predator-prey complex associated with larval capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci 39:991–1003.

GROVER, J. J., AND B. L. OLLA.

1986. Morphological evidence for starvation and prey size selection of sea-caught larval sablefish, *Anoplopoma fimbria*. Fish. Bull., U.S. 84:484–489.

HEMPEL, G., AND H. WEIKERT.

1972. The neuston of the subtropical and boreal Northeastern Atlantic Ocean. A review. Mar. Biol. (Berl.) 13:70–88.

HJORT, J.

1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Réun. Comm. int. Explor. Sci. Mer 20:1–228.

HUYER, A., R. D. PILLSBURY, AND R. L. SMITH.

1975. Seasonal variation of the alongshore velocity field over the continental shelf off Oregon. Limnol. Oceanogr. 20:90–95.

IKEDA, M., AND W. J. EMERY.

1984. Satellite observations and modeling of meanders in the California Current system off Oregon and Northern California. J. Phys. Oceanogr. 14:1434–1450.

JACOBY, C. A.

1982. Behavioral responses of the larvae of *Cancer magister* Dana (1852) to light, pressure, and gravity. Mar. Behav. Physiol. 8:267–283.

JOHNSON, D. F., L. W. BOTSFORD, R. D. METHOT, JR., AND T. C. WAINWRIGHT.

1986. Wind stress and cycles in Dungeness crab (*Cancer magister*) catch off California, Oregon and Washington. Can. J. Fish. Aquatic Sci. 43:838–845.

KENDALL, A. W., JR., AND J. CLARK.

1982a. Ichthyoplankton off Washington, Oregon, and Northern California. April-May, 1980. Natl. Mar. Fish. Serv., Northwest Alaska Fish. Cent. Process. Rep. 82–11, 44 p.

1982b. Ichthyoplankton off Washington, Oregon and Northern California. August, 1980. Natl. Mar. Fish. Serv., Northwest and Alaska Fish. Cent. Process. Rep. 82–12, 43 p.

KINGSFORD, M. J., AND J. H. CHOAT.

1985. The fauna associated with drift algae captured with a plankton-mesh purse seine net. Limnol. Oceanogr. 30:618–630.

1986. Influence of surface slicks on the distribution and onshore movements of small fish. Mar. Biol. (Berl.) 91:161–171.

LAROCHE, J. L., AND S. L. RICHARDSON.

1979. Winter-spring abundance of larval English sole, *Parophrys vetulus*, between the Columbia River and Cape Blanco, Oregon, during 1972–1975, with notes on occurrences of three other pleuronectids. Estuarine Coastal Mar. Sci. 8:455–476.

LASKER, R.

1975. Field criteria for survival of anchovy larvae: the relation between the inshore chlorophyll layers and successful first feeding. Fish. Bull., U.S. 71:453–462.

1981. The role of a stable ocean in larval fish survival and subsequent recruitment. *In* R. Lasker (editor), Marine fish larvae. Morphology, ecology and relation to fisheries, p. 80–87. Wash. Sea Grant Program, Univ. Wash. Press, Seattle.

LOUGH, R. G.

1976. Larval dynamics of the Dungeness crab, *Cancer magister*, off the central Oregon coast, 1970–71. Fish. Bull., U.S. 74:353–375.

MOOERS, C. N. K., AND A. R. ROBINSON.

1984. Turbulent jets and eddies in the California Current and inferred cross-shore transport. Science 223:51–53.

MUNDY, B. C.

1983. Yearly variation in the abundance and distribution of fish larvae in the coastal zone off Yaquina Head, Oregon, from June 1969 to August 1972. M.S. Thesis, Oregon State Univ., Corvallis, OR, 158 p.

MURPHY, G. I., AND R. I. CLUTTER.

1972. Sampling achovy larvae with a plankton purse seine. Fish. Bull., U.S. 70:789–798.

OWEN, R. W.

1982. Fronts and eddies in the sea: Mechanisms, interactions and biological effects. *In* A. R. Longhurst (editor), Analysis of marine ecosystems, p. 197–233. Acad. Press, N.Y.

PARRISH, R. H., C. S. NELSON, AND A. BAKUN.

1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175–203.

PETERSON, W. T., C. B. MILLER, AND A. HUTCHINSON.

1979. Zonation and maintenance of copepod populations in the Oregon upwelling zone. Deep-Sea Res. 26:467–494.

REILLY, P. N.

1983a. Dynamics of Dungeness crab, *Cancer magister*,

larvae off central and northern California. *In* P. W. Wild and R. N. Tasto (editors), Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery, p. 57–85. Calif. Dep. Fish game, Fish Bull. 172.

1983b. Predation on Dungeness crabs, *Cancer magister*, in central California. *In* P. W. Wild and R. N. Tasto (editors), Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery, p. 155–164. Calif. Dep. Fish. Game, Fish Bull. 172.

RICHARDSON, S. L.

1973. Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 71:697–711.

1980. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington. Fish. Bull., U.S. 78:855–877.

RICHARDSON, S. L., J. L. LAROCHE, AND M. D. RICHARDSON.

1980. Larval fish assemblages and associations in the northeast Pacific Ocean along the Oregon coast, winter-spring, 1972–1975. Estuarine Coastal Mar. Sci. 11:671–699.

RICHARDSON, S. L., AND W. G. PEARCY.

1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75:125–146.

SHANKS, A. L.

1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13:311–315.

1985. Behavioural basis of internal-wave-induced shoreward transport of megalopae of the crab *Pachygrapsus crassipes*. Mar. Ecol. Prog. Ser. 24:289–295.

SHENKER, J. M., AND B. L. OLLA.

1986. Laboratory feeding and growth of juvenile sablefish, *Anoplopoma fimbria*. Can. J. Fish. Aquat. Sci. 43:930–937.

SINCLAIR, M. F., M. J. TREMBLAY, AND P. BERNAL.

1984. El Niño events and variability in a Pacific mackerel (*Scomber japonicus*) survival index: support for Hjort's second hypothesis. Can. J. Fish. Aquat. Sci. 42:602–608.

SMALL, L. F., AND D. W. MENZIES.

1981. Patterns of primary productivity and biomass in a coastal upwelling region. Deep-Sea Res. 28:123–149.

SMITH, P. E.

1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849–874.

STEINER, W. W., J. J. LUZCKOVICH, AND B. L. OLLA.

1982. Activity, shelter usage, growth and recruitment of juvenile red hake, *Urophycis chuss*. Mar. Ecol. Prog. Ser. 7:125–135.

STEINER, W. W., AND B. L. OLLA.

1985. Behavioral responses of prejuvenile red hake, *Urophycis chuss*, to experimental thermoclines. Environ. Biol. Fish 14:167–173.

WINTER-TIME DISTRIBUTION AND ABUNDANCE OF COPEPOD NAUPLII IN THE NORTHERN GULF OF MEXICO

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ABSTRACT

Copepod nauplii were collected from continental shelf waters in 3 regions of the northern Gulf of Mexico during winters between 1981 and 1984, off Cape San Blas, Florida, off the Mississippi River delta, and off of Galveston, Texas. Some statistically significant ($P < 0.05$) patterns in the abundance and distribution of nauplii were observed: there was significant interannual variability in naupliar concentrations within the region around the Mississippi River delta; naupliar concentrations in the upper 10 m decreased in the onshore-offshore direction in 2 of 4 comparisons; naupliar concentrations in the upper 10 m differed regionally in 2 of 3 comparisons; and naupliar concentration was correlated with chlorophyll concentration in 4 of 5 comparisons.

Maximum concentrations of nauplii (number per m^3) within a water column were 2–10 times greater at stations influenced by the Mississippi River plumes than in the other 2 regions. This condition in attributed to vertical stratification imparted to the water column by the inflowing low salinity water from the Mississippi River. We conclude that the physical stratification provides a mechanism for the establishment of high concentrations of nauplii that otherwise would not exist in the winter months on the continental shelf.

Microzooplankton are important diet items for larval fish (Arthur 1976; Gamble et al. 1981; Checkley 1982; Govoni et al. 1983; Houde and Lovdal 1984; Stoecker and Govoni 1984), and gut analyses indicate that copepod nauplii are frequently the dominant prey form found in the larvae of many fish species (Duka and Gordina 1973). Available concentrations of microzooplankton are considered an important determinant of larval survival rates in the ocean because this relationship has been demonstrated in the laboratory (Laurence 1974; Houde 1978) and because field studies have demonstrated a relationship between regions or periods of high microplankton and high larval abundance (Arthur 1977; Lasker 1978). Because survival is enhanced by increased food availability, oceanographic processes that result in increased concentration or production of prey items are important.

The gulf menhaden, *Brevoortia patronus* (Clupeiformes), supports the largest volume fishery in the United States (U.S. Department of Commerce 1983). Spawning occurs in the wintertime, from October to March, in continental shelf waters of the northern Gulf of Mexcio (Fore 1970; Lewis and Rothmayr 1981; Warlen 1988), primarily off of Mississippi and Alabama to the east of the Mississippi River delta, and off of Louisiana to the west of the delta. During February and December 1982, concentrations of menhaden larvae in the region near the Mississippi River delta were greater in plume waters than outside and were much higher at the plume front (Govoni and Hoss[3]). Furthermore, gut contents of these larvae indicated that nauplii were the most abundant prey items.

Much of the continental shelf water of the northern and western Gulf of Mexico is vertically unstratified during the winter, and winter is also the season of minimum primary productivity in these regions, as it is in shelf waters of the northeast and southeast United States. However, coastal waters and nearshore regions influenced by freshwater inputs can be physically stratified during winter when low salinity plumes disperse over higher salinity shelf waters. We postulated that shelf waters influenced by fresh water from the Mississippi River plumes would be regions of increased production and concentration of microzooplankton. The purpose of this paper is to examine this hypothesis by describing the vertical and horizontal distribution and abundance of copepod nauplii in shelf waters of the northern Gulf of

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Mexico and by comparing these with oceanographic and hydrographic indicators of water column stratification and productivity.

METHODS

Samples were collected during 5 winter cruises between November and March, during 1981–84, (Table 1). Microplankton samples and hydrographic data were collected from 3 general regions of the northern Gulf of Mexico: off of Galveston, TX, in the region of the Mississippi River delta, and off of Cape San Blas, FL (Fig. 1). Samples were not collected from all 3 regions on each cruise.

Water samples for chlorophyll and nutrient analyses were collected with Niskin bottles. For each chlorophyll analysis, between 25 and 150 mL of seawater was filtered onto a GF/F or GF/C glass fiber filter and homogenized by grinding in 90% aqueous acetone. Fluorescence of the filtrate, brought up to a volume of 10.0 mL, was determined before and after acidification with 2 drops of 10% HCl using a Turner Designs[4] Model 10 fluorometer. Chlorophyll and pheopigment concentrations as chlorophyll equivalents were determined from

$$\text{chlorophyll } (\mu g/L) = \frac{K(f_o - f_a)}{v}$$

$$\text{pheopigment } (\mu g/L) = \frac{K(Rf_a - f_o)}{v}$$

where K is the machine calibration constant, f_o and f_a are the fluorescence readings before and after acidification, R is the acid ratio, and v is the volume of seawater filtered, in mL (Strickland and Parsons 1968).

Samples for nutrient analyses were frozen. Nitrate and nitrite were analyzed according to method number 353.2 described by EPA publication number EPA 600/4-79-020 (Environmental Protection Agency 1979).

Temperature and salinity were measured by several methods. During cruise I, temperature was measured by the temperature sensor on the MOCNESS[5] net, and salinity was measured with a refractometer. During cruises II and III, temperature was measured with expendable bathythermographs (Sippican Instruments). Salinity was measured with a YSI Model 33-S-C-T salinometer on cruise II, and with a Beckman Model RS5-3 salinometer on cruise III. For both of these cruises, bottle samples, analyzed in the laboratory with a Guildline Model 8400A Autosal, were used to check the shipboard salinity measure-

TABLE 1.—Station information, 1981–84.

Station	Date	Time	Depth (m)	Lat. (N)	Long. (W)
I–1	2–13–81	0000	18	29°05′	94°07′
I–2	2–13–81	1200	18	29°06′	94°07′
I–3	2–14–81	0001	90	28°04′	93°03′
I–4	2–14–81	1200	90	28°04′	93°03′
I–5	2–15–81	0000	180	27°54′	92°51′
I–6	2–15–81	1200	180	25°54′	92°50′
I–7	2–16–81	0001	180	28°34′	89°37′
I–8	2–17–81	1200	180	28°35′	89°38′
I–9	2–18–81	0001	90	28°50′	89°16′
I–10	2–18–81	1200	90	28°50′	89°16′
I–11	2–19–81	0000	18	28°56′	89°29′
I–12	2–19–81	1200	18	28°56′	89°29′
I–13	2–20–81	0000	90	29°09′	85°56′
I–14	2–21–81	1200	90	29°08′	85°56′
I–15	2–22–81	0000	180	29°28′	86°07′
I–16	2–22–81	1200	180	29°28′	86°07′
I–17	2–23–81	0001	18	29°36′	85°47′
I–18	2–23–81	1200	18	29°35′	85°47′
I–19	2–24–81	0001	18	30°12′	87°06′
II–1	12–05–82	0700	25	28°53′	89°29′
II–2	12–05–82	1255	62	28°53′	89°32′
II–3	12–05–82	1945	33	28°59′	89°34′
II–4	12–06–82	2120	887	28°20′	89°27′
II–5	12–07–82	0715	885	28°20′	89°27′
II–6	12–07–82	1220	834	28°19′	89°25′
II–7	12–08–82	1820	443	28°32′	89°53′
II–8	12–09–82	0830	402	28°34′	89°53′
II–9	12–09–82	1215	461	28°32′	89°53′
II–10	12–13–82	1245	44	29°26′	85°53′
II–11	12–15–82	1930	19	28°54′	89°29′
II–12	12–16–82	0900	68	28°51′	89°32′
III–1	11–19–83	1200	27	28°54′	89°29′
III–2	11–20–83	0800	35	28°47′	89°59′
III–3	11–20–83	1946	732	28°38′	89°00′
III–4	11–21–83	0555	27	28°54′	89°30′
III–5	11–22–83	1100	48	28°51′	89°30′
III–6	11–23–83	0500	194	28°31′	89°37′
III–7	11–24–83	1030	50	28°50′	89°31′
III–8	11–25–83	0820	45	28°55′	89°34′
III–9	11–25–83	1945	40	28°56′	89°36′
III–10	11–26–83	1200	16	28°54′	89°29′
III–11	11–27–83	0900	9	29°02′	89°30′
III–12	11–28–83	0840	29	28°48′	89°57′
III–13	11–28–83	1250	44	28°56′	89°51′
III–14	11–29–83	0950	24	29°03′	89°39′
III–15	11–30–83	0930	44	28°47′	89°58′
III–16	12–01–83	0800	38	28°52′	89°29′
IV–1	3–14–83		53	27°58′	95°53′
IV–2	3–19–83		59	28°18′	90°41′
V–1	2–21–84	0850	18	28°54′	90°25′
V–2	2–22–84	0830	18	28°54′	90°25′
V–3	2–23–84	0910	18	28°54′	90°25′
V–4	3–1–84	0835	18	28°54′	90°25′
V–5	3–1–84	0830	18	28°54′	90°25′
V–6	3–3–84	0730	18	28°54′	90°25′

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]Multiple opening-closing net and environmental sensing system.

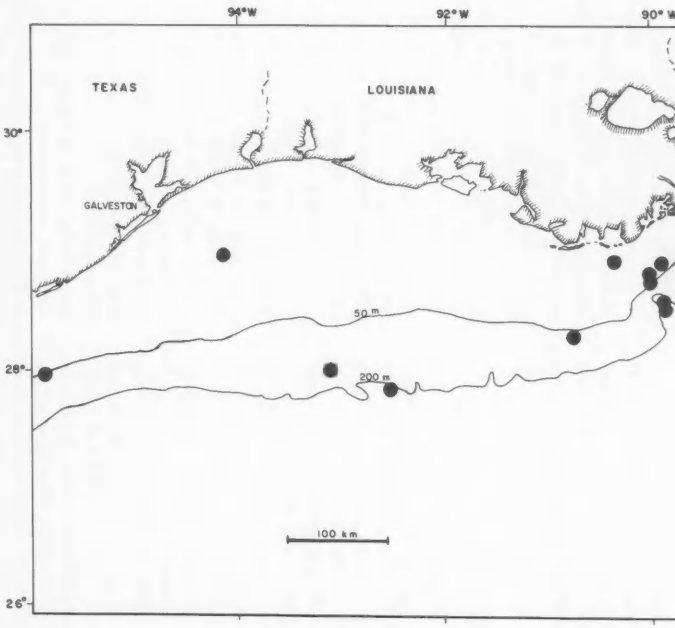

FIGURE 1.—St

1.—Station Locations.

ments. On cruise IV, a Plessey Model 9040 CTD was used for both temperature and salinity. On cruise V, salinity samples were stored in bottles and analyzed in the laboratory using a Guildline Model 8400A Autosal, and temperature was measured with reversing thermometers.

Microzooplankton were collected using 5 L (cruises I, II, and V) or 30 L (cruises III and IV) Niskin bottles. During cruise I, 1 L samples of untreated water were collected from 3 depths and preserved for later analysis. During subsequent cruises, samples were collected from up to 8 depths; four liters were poured gently through a 20 μm sieve, backwashed with filtered seawater into a sample jar, and preserved in a 5% formalin-seawater solution. In the laboratory, all organisms in each preserved sample were identified and counted. In selected samples, the length and width of the first 50 copepod nauplii were measured using an ocular micrometer. In addition, during cruise I larger nauplii were collected with 0.1 m^2 64 μm mesh nets nested inside the 1 m^2 333 μm mesh nets of a MOCNESS net (Wiebe et al. 1976). Estimates of naupliar abundance from these collections were used separately in the analyses for patterns in distribution and abundance. Lastly, from cruise I, the total number of copepods in the shallow-water samples, total number of copepods from the 333 μm nets, and the zooplankton displacement volume from the 333 μm nets were analyzed for patterns in distribution and abundance.

RESULTS

Samples from the Mississippi River delta region, collected during 1981 (cruise I), 1982 (cruise II), and 1983 (cruise III), were compared to determine if there was significant interannual variability within a region. Whole water samples and samples retained on 20 μm mesh sieves were pooled for this analysis under the assumption that nauplii in a whole water sample would be retained on a 20 μm mesh screen. The 64 μm net samples were excluded from this analysis. This test was made using average naupliar concentrations in the upper 10 m only; naupliar concentrations were typically lower in deeper waters, and we did not have the same number of deep and shallow stations for each of the 3 sampling years. A 1-way analysis of variance indicated significant variation between years within the Mississippi River delta region ($P < 0.01$). All 3 years were statistically different. These results indicated to us that regional or other spatial comparisons can only be made using samples collected during the same year. Interannual comparisons for other regions were not possible.

Samples were collected from all 3 regions during cruise I. Four tests for regional differences during this cruise were made. First, regions were compared based on naupliar concentrations in the upper 10 m only (Table 2); based on whole water collections F was significant at $P < 0.05$ and based on samples collected with 64 μm mesh nets F was significant at $P < 0.09$. Second, regions were compared based on naupliar concentrations from all depths (Table 2); based on whole water collections F was significant at $P < 0.01$ and based on samples collected with 64 μm mesh nets F was significant at $P < 0.22$. Thus, whole water samples collected on cruise I indicated significant regional differences in naupliar concentration but samples collected with 64 μm mesh nets did not. In addition, there were significant regional differences in the concentrations of total copepods ($P < 0.01$) and in zooplankton displacement volume ($P < 0.05$) during cruise I (data not shown). Regional comparisons were not possible during other cruises because all 3 regions were not sampled in years other than 1981.

Where possible, we also tested for onshore-offshore gradients in naupliar concentrations in the upper 10 m. Stations were categorized according to bottom depth as shallow, <18 m, intermediate, 18–90 m, and deep, >90 m, and comparisons were made between these 3 depth categories. A highly significant onshore-offshore difference existed during cruise I for nauplii collected with the 64 μm MOCNESS nets (Table 3). During cruise III samples were only collected in the Mississippi River delta region but onshore-offshore differences within this region were significant (Table 3). No significant onshore-offshore gradients were observed in naupliar concentrations determined from whole water samples collected from all 3 regions during cruise I, or in nauplii from only the Mississippi River delta region during cruise II (Table 3).

Although regional differences in average concentrations of nauplii were not strong, the vertical distributions were different. For example, several stations at approximately the 50 m isobath are compared in Figure 2. At station IV-1 (Fig. 2a) off the coast of Texas, there was no marked vertical heterogeneity in naupliar concentrations, the maximum concentration was low (23 nauplii/L), and the average concentration was

TABLE 2.—Regional comparisons of naupliar concentrations during cruise I. Samples were collected by 2 methods: whole water samples were collected with Niskin bottles, and 64 μm mesh nets were used to collect the net caught samples.

Cruise	Depths	Sample type	*n*	Probability of *F*
I	upper 10 m	whole water	28	< 0.05
I	upper 10 m	64 μm nets	126	< 0.09
I	all depths	whole water	57	< 0.01
I	all depths	64 μm nets	222	< 0.22

TABLE 3.—Onshore-offshore comparisons of naupliar concentrations from the upper 10 m of each station. Tests for cruise I are based on naupliar concentrations from all 3 regions pooled then separated into 3 depth categories. During cruises II and III, nauplii were only collected from the Mississippi River delta region.

Cruise	Regions	Sample type	*n*	Probability of *F*
I	all	whole water	28	< 0.14
I	all	64 μm nets	126	< 0.01
II	Mississippi R.	20 μm sieve	28	< 0.25
III	Mississippi R.	20 μm sieve	49	< 0.01

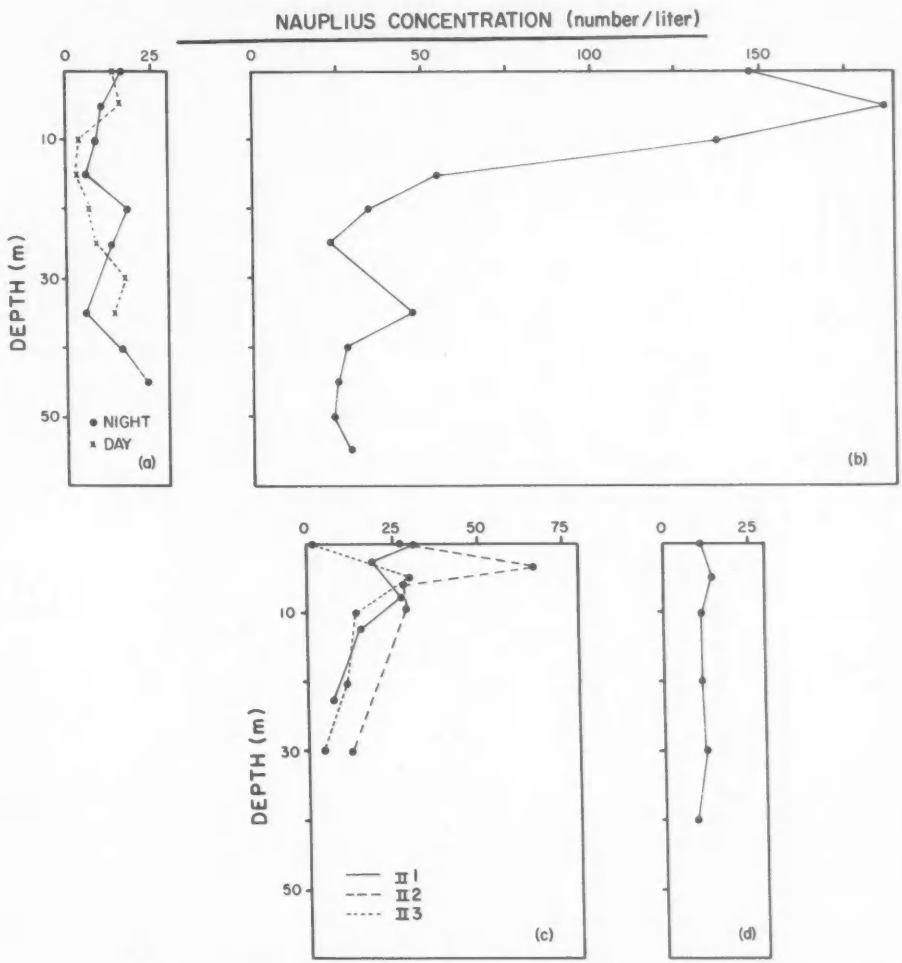

FIGURE 2.—Naupliar concentrations (number/liter) from selected stations near the 50 m isobath on the Texas continental shelf (a, station IV-1), the Louisiana Shelf (b, station IV-2, c, stations II-1, II-2, II-3), and the northwest Florida shelf (d, station II-10).

low (11 nauplii/L). The same pattern was observed off Cape San Blas (Fig. 2d); there was no marked vertical heterogeneity, and the maximum and average concentrations were low, 14 and 12 nauplii/L. In contrast, nauplii at stations near the 50 m isobath in the region near the Mississippi River delta typically showed marked vertical heterogeneity in abundance. At station IV-2 (Fig. 2b), the maximum concentration was 187 nauplii/L and the minimum was 24 nauplii/L. At station II-1, II-2, and II-3 in the Mississippi River delta region (Fig. 2c) naupliar abundances were also vertically heterogenous, although concentrations were lower than at Station IV-2. In general, based on all our vertical profiles (most not shown), regions influenced by the Mississippi River can contain high concentrations of nauplii in the surface layer, while subsurface concentrations are similar to concentrations in the other 2 regions.

Vertical structure in the distribution of nauplii appears to be related to physical structure. At the stations off the coasts of Texas and Florida (Fig. 2a, 2d), temperture and salinity were essentially vertically homogenous (Fig. 3a, 3d) whereas off the Mississippi River delta temperature and

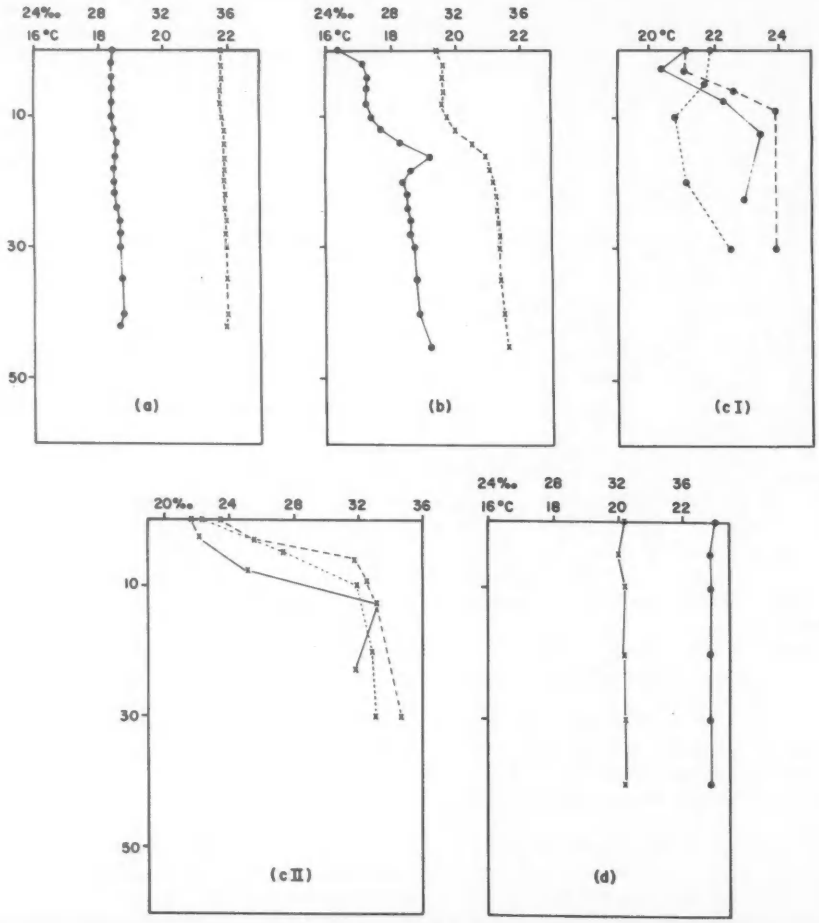

FIGURE 3.—The vertical distribution of temperature (•) and salinity (×) at the stations represented in Figure 2.

salinity were vertically stratified (Fig. 3b, 3c). The same pattern was seen in the chlorophyll a distributions (Fig. 4) and the nitrate distributions (Fig. 5).

Correspondence between chlorophyll a concentration and naupliar abundance was computed; the correlation coefficient for a linear regression of chlorophyll concentration on naupliar abundance for all 5 cruises (n = 269) was 0.39, significant at the 1% level. However, analysis of covariance showed that the relationship between chlorophyll and naupliar concentration was significantly different between cruises, and therefore the data from the 5 cruises should not be pooled. Although a significant relationship between chlorophyll concentration and naupliar concentration typically exists, it is not consistent from cruise to cruise. Regression parameters and correlation coefficients for each cruise are shown in Table 4. Pairwise tests indicate that the slope of the regression for cruise V was significantly different from all the others, cruise IV was differ-

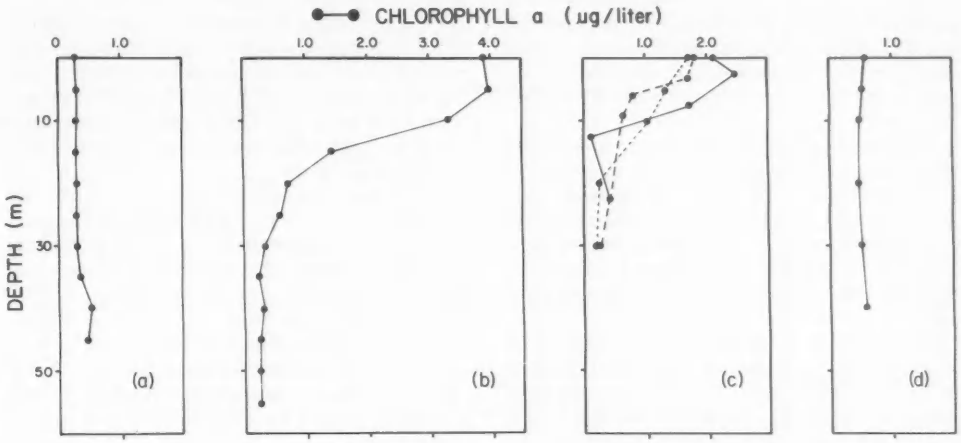

FIGURE 4.—The vertical distribution of chlorophyll a at the stations represented in Figure 2.

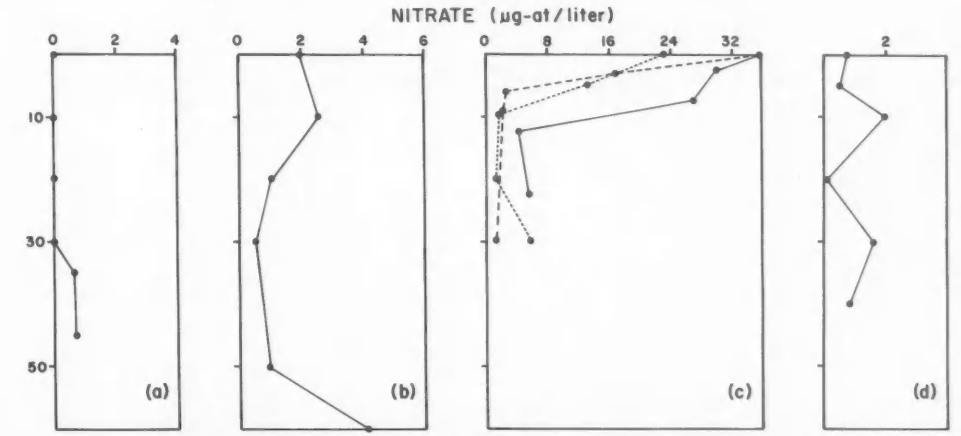

FIGURE 5.—The vertical distribution of nitrate at the stations represented in Figure 2.

TABLE 4.—Parameters and coefficients for linear regressions of chlorophyll concentration on nauplius concentration for each cruise. $Y = a + b(X)$ where Y = naupliar concentration as number per liter, and X = chlorophyll concentration as μg per liter. Significance level tested is 0.01.

Cruise	n	Intercept	Slope	Significance of slope	r^2	Significance of correlation
I	57	12.9	9.7	<0.01	0.40	<0.01
II	70	5.4	15.4	<0.01	0.53	<0.01
III	80	3.7	9.2	<0.01	0.34	<0.01
IV	20	6.9	39.4	<0.01	0.94	<0.01
V	42	26.1	1.1	NS	0.04	NS

ent from all others, cruise II was different from all the others, and cruises I and III were not different from each other but different from cruises II, IV, and V. The slopes of all relationships except cruise V were significantly different from zero.

The size-frequency distribution of nauplii did not vary in any systematic manner (Fig. 6). For example, at station IV-1, the bulk of the nauplii were between 20 and 100 μm at all depths sampled during both the daytime and nighttime periods. The size-frequency distribution was essentially identical at station IV-2, off Louisiana (data not shown).

At some stations, copepodid stages <600 μm in length (50–200 μm in width) were counted in addition to nauplii because they are potential prey items for menhaden larvae. Copepodites were usually not as abundant as nauplii, especially at stations with high naupliar abundances. On occasion, they were as abundant or, at specific depths, more abundant than the nauplii (Table 5). The ratio of nauplii to copepodites varied widely, between 16.3 and 0.3, so it is not possible to assign a constant factor to naupliar abundances to estimate the increase in available prey attributable to copepodid stages.

Other microzooplankton were usually not as abundant as nauplii or copepods. In our samples, various forms of eggs reached a maximum density of 6 eggs/L (cruise III station 6 at 3 m, data not shown). Pelecypod larvae at one station (III-11) were abundant, reaching a maximum of 29 larvae/L at 4 m, compared with 22 nauplii, 7 copepodites, and 2 eggs/L in the same sample. Only on this one occasion were organisms other than copepodites or nauplii the dominant form of microzooplankton.

TABLE 5.—Abundance (number/liter) of other microzooplankton in addition to nauplii at selected stations during cruise III.

Station	Depth (m)	Nauplii	Copepodids <600 μm	Copepodids >600 μm	Larvaceans	Eggs	Other
III–3	6	17.3	7.5	1.0	7.8	0.5	1.8
	9	29.3	12.0	0.5	11.0	0	1.8
	12	17.5	8.0	1.0	6.8	1.5	2.3
	20	7.8	2.8	0	1.0	2.0	0.5
III–7	0	24.0	6.3	4.0	0	1.0	1.0
	3	15.3	12.3	1.0	0	0.3	1.3
	5	3.0	5.0	1.0	0	0.8	0.3
	13	4.8	5.8	0.3	0	0	0.5
	22	2.0	1.0	0.3	0	0	0
III–14	0	15.8	12.0	1.3	0	1.3	2.0
	5	44.8	3.8	0.3	0.5	3.0	4.0
	10	40.0	6.8	0.8	1.3	4.3	0.3
	15	11.5	8.0	3.8	1.0	1.8	0.3
	20	12.0	35.0	6.8	0.3	0.3	0.8
III–16	0	15.8	25.3	5.0	0	0	12.8
	6	8.0	16.0	2.3	0	1.0	2.5
	9	30.0	14.0	2.0	0	0.3	2.5
	12	29.0	13.3	0.5	0	0.8	1.3
	15	17.0	12.5	1.0	0	0.8	0.5
	25	31.8	12.8	0.8	0	0	5.0

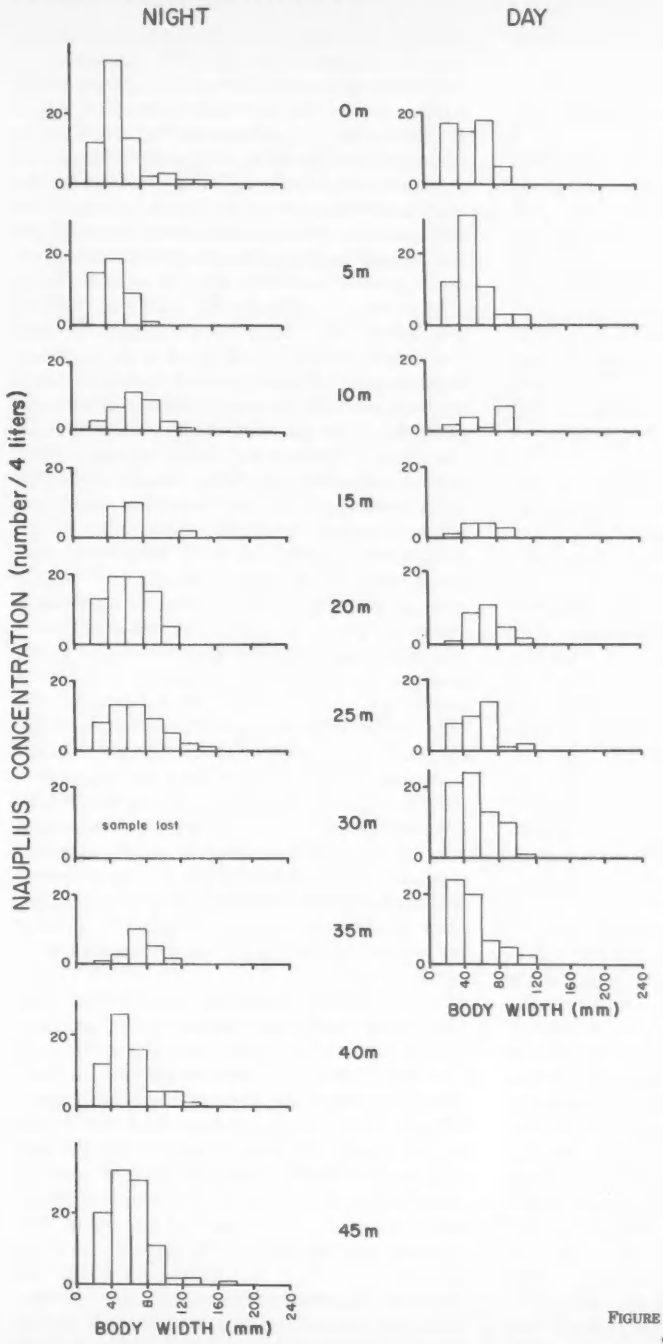

FIGURE 6.—The size-frequency distribution of nauplii from station IV-1.

DISCUSSION

Menhaden larvae between 3 and 20 mm long collected during wintertime from 3 regions in the northern Gulf of Mexico contained a variety of diet items, including dinoflagellates, tintinnids, copepod eggs, nauplii, copepodids, juvenile pelecypods, and pteropods (Govoni et al. 1983, 1985). Dinoflagellates and tintinnids constituted the main diet items of larvae <5.0 mm long but were replaced by copepod nauplii, then copepodids and small adult copepods as larvae grew larger.

In another study, Stoecker and Govoni (1984) found that copepod nauplii were the dominant items in the diet of menhaden larvae 7.0–9.0 mm long, although only 12 fish were examined. Later studies, however, have verified that nauplii are the dominant items in the diet of a wide size range of larval menhaden collected in the boundary between the plume of the Mississippi River and oceanic waters (Govoni and Hoss fn. 3)

The maximum width of food items in menhaden larvae <5 mm long was about 200 μm (Govoni et al. 1983). This width increased up to about 400 μm for larvae 10 mm long. In another study (Stoecker and Govoni 1984) maximum prey size was calculated in a different manner; the average width of the largest prey type was used. With this index the estimated maximum width of prey items was 50 μm for larvae <5 mm long and about 140 μm for larvae 9–11 mm long. In our study, most of the nauplii were between 40 and 80 μm body width, and most of the copepodites were between 50 and 200 μm body width. These copepod developmental stages were in the size range of diet items typically found in guts of intermediate size (7–11 mm) larvae of the gulf menhaden and we believe our samples are reasonably representative of the prey concentrations available to these larvae. Other prey items for larvae in this size range were common only on rare occasions.

The importance of high prey concentrations to successful feeding and survival of fish larvae has frequently been noted (Hunter 1981). Concentrations required to give high survival in laboratory experiments are seldom found in the ocean but careful attention to culture techniques can result in reasonably high survival at prey densities that are close to or overlap the maximum natural concentrations (Houde 1978). At stations near the river delta that are strongly affected by the river plumes, maximum concentrations of nauplii were typically in the range of 20–50 nauplii/L. At stations farther down plume, away from the delta, maximum naupliar concentrations were higher, up to 187 nauplii/L at station IV-2 for example. It is not clear whether this is a seasonal pattern, a pattern due to the down-plume development of the food web, or a pattern attributable to some other factors. However, the concentrations observed in waters with salinities lowered by the river plumes are mostly within the range of 10–100 nauplii/L that is frequently reported for oceanic and coastal waters for microzooplankton, or the 50–100 nauplii/L range for coastal and estuarine areas (see Houde 1978; Hunter 1981 for summaries). The addition of copepodite stages and other potential prey items to the naupliar abundances in this study would increase the estimates of available prey somewhat but usually not more than 20%. At least during the wintertime, the waters surrounding the Mississippi River delta do not appear to contain exceptionally high concentrations of copepod nauplii, compared to other coastal and estuarine areas.

The vertical distribution of nauplii was frequently similar to that of chlorophyll. Regressions of naupliar concentration on chlorophyll concentration were significant for 4 of the 5 cruises although not the same in each case. Assuming chlorophyll is a reasonable indicator of phytoplankton abundance and thus food abundance for nauplii, then nauplii appear to be aggregated at the depth of highest food availability. Year to year variability in the relationship indicates that other factors are also important in determining the abundance and distribution of nauplii. Because eggs released from adult female copepods would sink out of the surface water before hatching, it is probable that active swimming by nauplii plays a part in the aggregation process, perhaps enchanced by physical convergence processes.

In our study we noted that there were interannual differences in naupliar concentrations, there were sometimes significant regional differences, and there were sometimes significant onshore-offshore differences. Although we anticipated finding higher concentrations of nauplii in the region near the Mississippi River delta, this pattern was not always observed. This finding might indicate that there is not an important difference between the 3 regions as far as larval food availability is concerned. Alternatively, it might indicate that there are subregions within the larger Mississippi River delta region that contain a food environment for fish larvae that allows for enhanced survival and growth, but that we failed

to clearly identify and segregate these regions. The overall region did not always appear significantly better than the other regions because only parts of it are better.

On the continental shelf in the Gulf of Mexico, as in other shelf regions of the United States, the typical pattern is for the water to be vertically well-mixed during the wintertime (Parker 1968). Autumn cooling breaks down the thermal stratification that has existed throughout the summer and allows the isothermal water column to be easily mixed. The major exception to this general pattern in the Gulf of Mexico is the shelf region influenced by the large volume of freshwater runoff from the Mississippi River. During this period, the freshwater influx is of sufficiently large volume (average flow for December to March in 1975 through 1979 was 17,290 m^3/second (U.S. Army Engineer District, New Orleans Corps of Engineers, 1980)) to physically stratify the shelf waters hundreds of km downstream from the delta. We suggest that this salinity-induced stratification is a vital component of the recruitment success of Gulf menhaden because it provides an environment in which prey aggregations can occur. It has been suggested that vertical stratification by other small-scale physical phenomena (e.g., Langmuir circulation) allows significant patchiness of prey items to exist (Lasker 1975). This patchiness provides small regions of comparatively high food concentrations for fish larvae, and results in improved feeding success. In this study, copepod nauplii were aggregated vertically at stations with physical stratification and were nearly homogenously distributed at stations lacking physical stratification. Maximum naupliar concentrations (no. per m^3) at stratified stations were typically 2–10 times greater than at nonstratified stations.

In conclusion, we believe that the large freshwater inflow of the Mississippi River during the wintertime spawning period of the Gulf menhaden contributes to the feeding success and survival of larval fish by providing physical stratification which in turn results in a vertical stratification of phytoplankton and microzooplankton in layers or patches of relatively high concentrations.

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LITERATURE CITED

ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull., U.S. 74:517–530.
1977. Distributions, size, and abundance of microcopepods in the California Current system and their possible influence on survival of marine teleost larvae. Fish. Bull., U.S. 75:601–611.

CHECKLEY, D. M., JR.
1982. Selective feeding by Atlantic herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. Mar. Ecol. Prog. Ser. 9:245–253.

DUKA, I. A., AND A. D. GORDINA.
1973. Abundance of ichthyoplankton and feeding of fish larvae in the western Mediterranean and adjacent areas of the Atlantic Ocean. Hydrobiol. J. 9:54–59.

ENVIRONMENTAL PROTECTION AGENCY.
1979. Methods of chemical analysis of water and wastes. Nitrogen, nitrate-nitrate. U.S. Environ. Prot. Agency, Cincinnati, OH 45268.

FORE, P. L.
1970. Oceanic distribution of eggs and larvae of the Gulf menhaden. Rep. Bur. Comm. Fish. Biol. Lab., Beaufort, NC, Fish. Wildl. Serv. Circ. 341.

GAMBLE, J. C., P. MACLACHLAN, N. T. NICHOLL, AND I. G. BAXTER.
1981. Growth and feeding of Atlantic herring larvae reared in large plastic enclosures. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:121–134.

GOVONI, J. J., A. J. CHESTER, D. E. HOSS, AND P. B. ORTNER.
1985. An obeservation of episodic feeding and growth of larvae *Leiostomus xanthrus* in the northern Gulf of Mexico. J. Plankton Res. 7:137–146.

GOVONI, J. J., D. E. HOSS, AND A. J. CHESTER.
1983. Comparative feeding of three species of larval fishes in the northern Gulf of Mexico: *Brevoortia patronus*, *Leiostomus xanthrus*, and *Micropogonias undulatus*. Mar. Ecol. Prog. Ser. 13:189–199.

HOUDE, E. D.
1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull. Mar. Sci. 28:395–411.

HOUDE, E. D., AND J. A. LOVDAL.
1984. Seasonality of occurrence, foods and food preferences of ichthyoplankton in Biscayne Bay, Florida. Estuarine Coastal Shelf Sci. 18:403–419.

HUNTER, J. R.
1981. Feeding ecology and predation of marine fish larvae. *In* R. Lasker (editor), Marine fish larvae. Morphology, ecology, and relation to fisheries, p. 34–77. Univ. Wash. Press, Seattle.

LAURENCE, G. C.
1974. Growth and survival of haddock (*Melanogrammus aeglefinus*) larvae in relation to planktonic prey concentration. J. Fish. Res. Board Can. 31:1414–1419.

LASKER, R.
1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453–462.
1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:212–230.

LEWIS, R. M., AND C. M. ROTHMAYR.
1981. Spawning and sexual maturity of gulf menhaden, *Brevoortia patronus*. Fish. Bull., U.S. 78:947–951.

PARKER, C. A.
1968. The effect of a cold air outbreak on the continental shelf waters of the northwestern Gulf of Mexico. Tech. Rep. 68-3T, 89 p. Off. Nav. Res.

STOECKER, D. K., AND J. J. GOVONI.
1984. Food selection by young larval gulf menhaden (*Brevoortia patronus*). Mar. Biol. 80:299–306.

STRICKLAND, J. D. H., AND T. R. PARSONS.
1968. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 167, p. 201–203.

U.S. DEPARTMENT OF COMMERCE.
1983. Fisheries Statistics for the United States, 1982.

U.S. ARMY ENGINEER DISTRICT, NEW ORLEANS CORPS OF ENGINEERS.
1980. Stages and discharges of the Mississippi River and its tributaries and other watersheds in the New Orleans District, 1975–1979.

WARLEN, S. M.
1988. Age and growth of larval menhaden, *Brevoortia patronus*, in the northern Gulf of Mexico. Fish. Bull., U.S. 86:77–90.

WIEBE, P. H., K. H. BURT, S. H. BOYD, AND A. W. MORTON.
1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. J. Mar. Res. 34:313–326.

THE EFFECTS OF SILTATION ON RECRUITMENT OF SPINY LOBSTERS, *PANULIRUS ARGUS*

WILLIAM F. HERRNKIND,[1] MARK J. BUTLER IV,[1] AND RICHARD A. TANKERSLEY[2]

ABSTRACT

Several surveys in the Florida Keys indicated fewer juvenile spiny lobsters, *Panulirus argus*, in an area where their primary habitat, stands of benthic algae *Laurencia* spp., was heavily silted as compared with similar, less silted habitat. We tested several hypotheses explaining this relationship: 1) planktonic postlarval lobster abundances are lower in the silted area, 2) siltation of algae impedes postlarval settlement or subsequent juvenile habitat selection, or 3) siltation increases mortality at the time of metamorphosis. We also compared the time-to-metamorphosis for settling pueruli within silted and nonsilted algae, analyzed the physical character of algal silt in low-silt and high-silt regions and measured the abundances of epifauna constituting prey of juvenile spiny lobsters. Planktonic postlarval abundances were substantially higher in the high-silt area thus rejecting hypothesis 1. Likewise, results from laboratory experiments testing the effect of algal siltation on postlarval time-to-metamorphosis and early postsettlement survival showed no short-term increase in mortality. Limited postlarval settlement and avoidance of silted algal habitats by juveniles, as determined in substrate choice experiments, probably accounts for the paucity of young spiny lobsters in heavily silted localities. In addition, although juvenile spiny lobsters are nonselective predators, lower prey availability in silted algae probably promotes transciency which, in turn, causes increased mortality by predation while juveniles are exposed. Large-scale siltation exacerbated by human activity must be viewed as potentially deleterious to spiny lobster recruitment.

The western Atlantic or Florida spiny lobster, *Panulirus argus*, is the focus of an intense commercial and recreational fishery in south Florida, particularly the Florida Keys. Besides severe fishing pressure, spiny lobster populations are subject to a variety of other factors that potentially limit population size. For example, habitat degradation, like that resulting from chronic siltation, may affect not only adult lobsters but the postlarval settlement stage as well. During 1983 and 1984 we sampled numerous sites in a region of about 40 km^2 east of Big Pine Key which was chronically heavily silted and held low numbers of newly settled spiny lobsters despite extensive benthic algal growth typical of settlement habitat. We hypothesized that postlarval spiny lobsters either do not settle in silted habitat or settle there but do not survive. In either case, we supposed that the heavy siltation reduced the carrying capacity of otherwise suitable habitat, potentially reducing regional recruitment where siltation is widespread.

Sediment particle size, composition, and stability influence larval settlement in a variety of marine benthic invertebrates (Crisp 1974, 1976; Gray 1974; Rhoads 1974; Pearson and Rosenberg 1978). For example, heavy siltation and sediment instability, created by natural biogenic reworking of the substrate and subsequent resuspension of sediments by turbulence reduces the abundance of suspension feeding infauna (Rhoads and Young 1971; Aller and Dodge 1974). In addition, siltation from human activities (e.g., dredging, shoreline development, boat traffic, etc.) can degrade benthic community structure via anaerobiosis, direct burial, toxic poisoning, or increased turbidity (Morton 1977; Allen and Hardy 1980; Jones and Candy 1981; Cortes and Risk 1985). Most available information concerns sessile or infaunal species, but little information exists for mobile, epibenthic forms (Pearson and Rosenberg 1978). Although the habitat selection and burrowing behavior of some shrimps and juvenile clawed-lobsters has been investigated in relation to substrate character (Ruello 1973; Howard and Bennett 1979; Aziz and Greenwood 1982; Botero and Atema 1982; Pottle and Elner 1982; Roach 1983; Herrnkind and Butler 1986), we know of no research describing the effect of siltation on deca-

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pod recruitment. Our research focuses on the impact of siltation on spiny lobster postlarvae and early benthic juveniles, stages that are morphologically and behaviorally distinct from adults.

Late stage *P. argus* phyllosome larvae drift in the oceanic plankton for 6–9 months after hatching and metamorphose offshore into nonfeeding pueruli (postlarvae) that swim inshore and settle in benthic vegetation (Marx 1986). Newly settled pueruli metamorphose into cryptically colored benthic juvenile instars after about one week. Pueruli preferentially settle in highly architectured benthic algal assemblages where subsequent survival and growth depend upon available prey and physical refuge from predators (Herrnkind and Butler 1986). Ubiquitous, widely distributed stands of bushy red algae, *Laurencia* spp., provide these essential conditions and probably serve as the most important regional settlement and nursery habitat for juvenile spiny lobsters (Marx and Herrnkind 1985a, b; Herrnkind and Butler 1986; Marx 1986). The early instars remain within the algae for several months until attaining about 20 mm carapace length (CL) (Andree 1981; Marx and Herrnkind 1985a) when they begin to occupy crevices in rubble or under sponges, coral, and exposed seagrass rhizome mats. In Florida, postlarval settlement is yearround with vernal, autumnal, newmoon, and occasionally aperiodic peaks (Little 1977; Little and Milano 1980; Marx 1986). The spatial pattern of settlement is poorly known although new recruits are widely dispersed within algal habitats; diver surveys have yielded estimates of one juvenile per 36 m^2 of profuse algal growth (Marx and Herrnkind 1985a). Yet because postlarvae settle continuously and juveniles grow rapidly, a single hectare of the above habitat is estimated to nurture about 1,000 spiny lobsters annually (Marx and Herrnkind 1985a; Marx 1986). There is no compelling evidence suggesting that benthic stage lobsters immigrate into Florida waters from other Caribbean areas, although their planktonic larvae presumably do so (Lyons 1980; Marx 1986). Recruitment is thus primarily limited to postlarval influx. Therefore, precise knowledge of the factors influencing postlarval recruitment and recruit mortality is essential to managing the intensive Florida spiny lobster fishery.

Here we report on studies undertaken to investigate the impact of the observed algal siltation on spiny lobster recruitment. We compared field abundances of both pueruli and early juveniles in a representative silted and unsilted area, examined the relationship between siltation and available epifaunal prey, determined the impact of silt load on puerulus survival from settlement through metamorphosis, and tested the preference of settling pueruli and algal-dwelling juveniles for silted and unsilted algae.

METHODS

Postlarval-Juvenile Abundance in Silted and Unsilted Habitats

During June through August 1985, we compared the natural abundance of newly settled juvenile spiny lobsters (6–20 mm CL) in previously sampled, chronically silted and unsilted areas. The silted site (No Name Key) was located approximately 30 m off the western shore of No Name Key (Monroe County, FL, U.S.A.) and the unsilted site (Burnt Point) 30 m off the northwest shore of Grassy Key at Burnt Point (Fig. 1). The benthic habitat at both sites was similar and characterized by nearly contiguous stands of algae (*Laurencia* spp.) at depths of 1.5–3.0 m. Intensive visual search in algal clumps by divers was used to estimate the relative number of benthic juveniles. Because newly settled spiny lobsters are almost exclusively found associated with algal clumps (Marx and Herrnkind 1985a), catch per unit effort (CPUE) as search time within algae, gives a more suitable estimate for our purposes of comparing abundance than density/area per se. Modified Witham-type postlarval collectors (Witham et al. 1964, 1968; Little and Milano 1980; Marx and Herrnkind 1985a) were used to compare postlarval abundance among sites. Twelve collectors were initially deployed at both sites and visited approximately every 2 weeks for 3 months. Collector results are reported in CPUE to standardize catch records biased by the loss of collectors and different sampling durations.

Algal Silt Content and Prey Content

To determine the amount of silt and macrofauna contained in algal clumps at the silted and unsilted sites, we bagged individual clumps (approximately 25 cm diameter) of *Laurencia* in the field for subsequent laboratory processing. Care was taken to ensure that loose silt present on the surface of the algae was not disturbed during collection. Ten clumps, ranging in displacement volume from 55 to 300 mL, were collected at each site. Algal samples were rinsed through a series

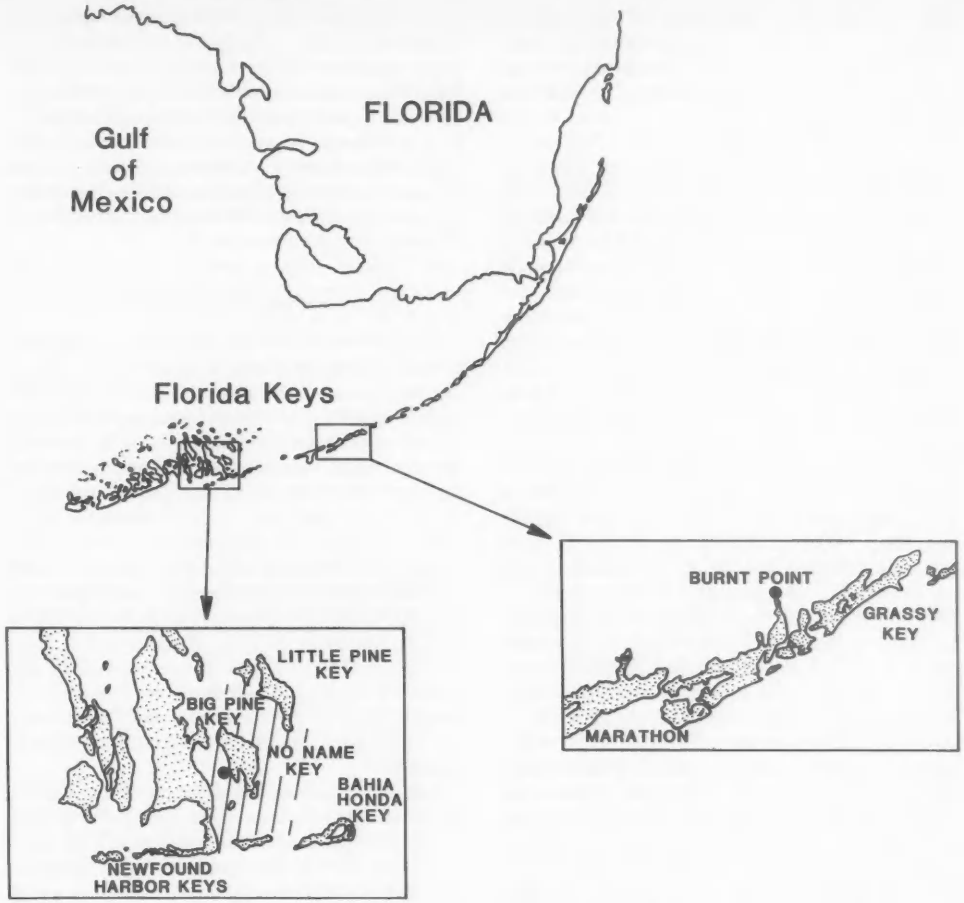

FIGURE 1.—Map of field sites in the middle and lower Keys, Monroe County, FL, U.S.A. Insets provide more detail of the areas surrounding our field sites (●). Diagonal lines depict approximate extent of the heavily silted area we surveyed.

of sieves (500 μ, 250 μ, and 63 μ; U.S. Standard Sieve Series), but only the two smallest size fractions were retained because subsamples >500 μ consisted entirely of shell and algae fragments. Silt samples were dried for 48 hours at 100°C and then weighed. The amount of algal-entrained silt at the two sites was compared using a two-sample t-test. Organic weight of the silt was derived by digesting three silt samples in 30% hydrogen peroxide for 1 week, then oven drying the remaining silt at 60°C for 48 hours (Cortes and Risk 1985). The fraction of carbonates in the silts was determined by dissolving the three samples in 5% hydrochloric acid for 1 week, then drying the samples as above (Cortes and Risk 1985). Percent organics and carbonates (by weight) in the silts at the two sites were compared in two-sample t-tests on arcsin transformed data.

We counted the number of epifaunal prey in silted and unsilted clumps to determine the possible influence of siltation on juvenile spiny lobster food abundance. The reported estimates of prey abundance are means of two separate counts per clump; 5 clumps per treatment were processed. The volume of each *Laurencia* clump was determined by water displacement, and all silt load

and prey abundance estimates standardized by clump volume. Prey abundance data were analyzed using a two-way fixed-effects ANOVA on log transformed data and Bonferroni pairwise multiple comparisons.

Habitat Selection/Settling Experiments

We tested postlarval settlement and juvenile habitat selection in laboratory experiments using clumps of *Laurencia* spp. with high- and low-silt loads (referred to hereafter as silted and unsilted); the null hypothesis being equal selection of both habitats. Experiments were conducted in fourteen 75.7 L aquaria with subgravel filters and circulating current of 3 cm s^{-1}. Light was provided by skylights and fluorescent lights with a photoperiod of approximately 14L:10D. Two 20 cm diameter algal clumps, one silted and one unsilted, were situated 25 cm apart at opposite ends of each aquarium and at least 5 cm from aquarium walls. The number of natural prey in both silted and unsilted clumps far exceeded the number eaten daily by a juvenile. To further control food availability in experiments with juveniles we added equal amounts (10 mg) of *Tetramin*[3] fish food to each clump, providing an overabundance of food available ad libitum. If juveniles chose one type of algal clump over the other, then their selection was most likely based on the presence or absence of silt, because food abundance and quality were similar, if not strictly identical, in both types of algal clumps. Pueruli neither feed nor respond to the differential abundance of potential prey (Herrnkind and Butler 1986). Silted algae was collected from the No Name Key site (see section on Algal Silt Content and Prey Content); unsilted algae was collected just offshore of the Sea World Marine Science and Conservation Center on Long Key. Fresh algal clumps were used in each experimental replicate. An experiment was initiated by introducing a single puerulus or juvenile spiny lobster to the center of an aquarium through a 5 cm diameter PVC pipe. Once a spiny lobster settled to the substrate, the pipe was slowly withdrawn allowing the lobster to move freely about the aquarium. This technique prevented "tailflipping" by lobsters and facilitated active selection of habitats. Twenty-four hours later we located the lobsters and recorded their positions, as in previous experiments (Herrnkind and Butler 1986). Fourteen spiny lobsters were tested on day 1, 14 more on day 2, and so on until our stock of animals was depleted. Each lobster was used only once. All pueruli were collected on the incoming tide from the plankton in interisland channels. Pueruli were either tested immediately or allowed to metamorphose for later use in experiments requiring juveniles. Data were analyzed with log-linear Goodness-of-fit tests.

Metamorphosis Experiment

The effect of siltation on the survival and time-to-metamorphosis of pueruli was tested experimentally in an outdoor, flow-through seawater system. One freshly collected puerulus was placed in each of 46 seawater-filled 1 L plastic beakers, 23 containing 5 cm diameter clumps of unsilted algae and the other 23 an equal amount of silted algae. Each container was independently supplied with flowing, filtered seawater. Algal clumps were replaced daily. Pueruli do not feed and their habitat selection operates independent of food availability (Herrnkind and Butler 1986), thus no food was added to the containers. Seawater temperature in the beakers remained between 26° and 28°C; photoperiod was approximately 14L:10D. Pueruli were monitored daily and their survival and time-to-metamorphosis recorded.

Pueruli were collected as transparent postlarvae from the plankton in interisland channels which concentrate oceanic postlarvae as they move into Florida Bay nursery areas. Time-to-metamorphosis values represent the elapsed time (in days) from puerulus collection until metamorphosis into the first benthic stage. Values are likely to differ among collections as different cohorts of pueruli arrive inshore. There are currently no techniques available to determine the actual age of pueruli (i.e., time since metamorphosis from the phyllosoma stage), but estimates of duration of the puerulus stage range from 2 weeks to 1 month (Lyons 1980; Calinski and Lyons 1983). Differences in time-to-metamorphosis between the two treatments were analyzed via a two-sample t-test.

Juvenile Spiny Lobster Prey Selection Experiments

Laboratory experiments were conducted to determine juvenile spiny lobster prey preference

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

and rate of consumption of algal epifauna. Prey were obtained by rinsing large clumps of *Laurencia* through a 100 μ sieve. Prey included small gastropods, amphipods, isopods, and ostracods ranging in size from 1 to 9 mm (Marx and Herrnkind 1985a). Prey were individually counted and placed in 1 L plastic beakers containing 750 mL of seawater. One starved (24-h) juvenile lobster (6–8 mm CL) was introduced to each container, allowed to feed for 12 hours, and was then removed; the remaining prey were counted. Fifteen spiny lobsters were tested in each experiment; each lobster was used once. Three experiments were conducted using different prey combinations (Table 1), but the total number of prey available remained similar and exceeded the amount a single lobster could consume in 12 hours. Electivity indices calculated for each experiment were used in multiple comparison tests to determine whether juvenile spiny lobsters fed preferentially or randomly (Johnson 1980).

TABLE 1.—Relative prey availabilities (A) and predator usage (U) values (percentages) in the three juvenile spiny lobster prey selection experiments. N = 15 lobsters per experiment. F-values calculated from Johnson (1980) indicate whether prey choice differed significantly from random in each trial; none of the tests were significant at $P = 0.05$.

	Experiment					
	1		2		3	
Prey type	A	U	A	U	A	U
Gastropoda						
Tricolia sp.	43.5	61.5	71.4	83.0	58.0	54.5
Battillaria spp.	8.7	1.0	4.3	0.2	—	—
Tegula spp.	6.5	0.0	—	—	—	—
Atys spp.	—	—	14.3	7.2	—	—
Amphipoda	32.6	33.9	10.0	9.6	7.0	7.1
Isopoda	—	—	—	—	17.4	20.0
Copepoda	—	—	—	—	11.6	13.1
Ostracoda	—	—	—	—	6.0	5.3
Decapoda	8.3	3.6	—	—	—	—
F-values	0.46		0.40		0.09	
df	4,11		3,14		4,11	

RESULTS

Postlarvae were more abundant on collectors at the silted site than at the unsilted site. Diver surveys revealed that higher numbers of algal-dwelling juveniles (<20 mm CL) resided at the unsilted site despite greater influx of pueruli into the silted area (Table 2). Only one juvenile spiny lobster collected at the silted site was <20 mm CL, most were considerably larger (25–35 mm CL) than those at the unsilted site, and some were possibly large enough to have immigrated there from adjacent unsilted areas.

Silt recovered from the algal clumps was largely calcareous and formed a cohesive cast around the algal filaments. Classifying algal-bound silts by particle size would yield irrelevant values because sieving caused fragmentation of aggregated particles. Therefore we report only the total dry weight of the silts. Algae at No Name Key carried a higher silt load than algae at Burnt Point ($\bar{x}$ = 125 vs. 65 g/L algae, respectively; $t = 2.90$, df = 18, $P < 0.01$). Silt at No Name Key was characterized as 12.5 ± 7.4% organic and 28.1 ± 27.6% carbonate by weight, whereas Burnt Point silt was 16.9 ± 1.06% organic and 66.3 ± 14.5% carbonate (means ± 1 SD). There was no significant difference in silt composition between sites (organics: $t = 0.83$, df = 4, $P > 0.05$; carbonates: $t = 1.97$, df = 4, $P > 0.05$), although sample sizes at each site were small and sample variance substantial. Algae at both sites contained primarily gastropods, amphipods, and isopods, although significantly more gastropods and echinoderms occupied unsilted clumps (Fig. 2, Table 3; $P < 0.05$ in Bonferroni pairwise multiple comparisons).

Significantly more pueruli settled in unsilted algal clumps than in silted clumps during laboratory settlement choice experiments (38 vs. 11, respectively; $G = 15.72$, $P < 0.001$). Juvenile spiny lobsters responded similarly in the habitat selection experiment (54 vs. 24; $G = 11.78$, $P < 0.001$). We excluded the open sand habitat in aquaria from our analysis because 1) juvenile spiny lobsters are never found residing on open sand in the field, presumably due to a lack of food and refuge

TABLE 2.—(A) Postlarval lobster abundances at silted and unsilted Florida Bay study areas. Postlarval catch per unit effort (CPUE) was estimated from Witham collector catches. (B) Juvenile lobster (8–20 mm CL) abundances at the two study sites in 1985 and adjacent areas sampled during 1983 and 1984. Juvenile CPUE was estimated via diver surveys.

A. POSTLARVAL ABUNDANCE

Location	Description	CPUE[1] June	July	August
No Name Key	silted	0.08	0.32	0.15
Burnt Point	unsilted	0.01	0.05	0.10

B. JUVENILE ABUNDANCES

Location	Description	Diving hours	CPUE[2]
No Name Key (1983–85)	silted	28	0.04
Burnt Point (1983–85)	unsilted	20	0.50

[1]CPUE = $\frac{\text{no. of postlarvae/no. of collectors}}{\text{no. of days between collections}}$

[2]CPUE = $\frac{\text{no. of lobsters collected}}{\text{no. of diver hours}}$

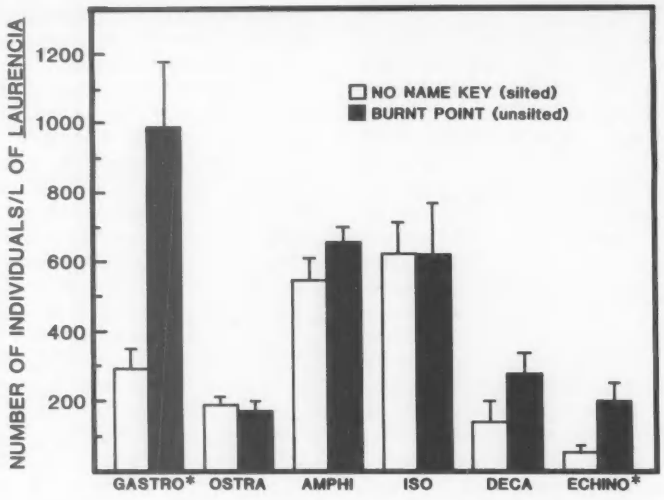

FIGURE 2.—Abundances ($\bar{x} \pm 1$ SE) of the six most common prey found in algal clumps at the silted No Name Key and unsilted Burnt Point sites. Five clumps were collected at each site. Values are standardized by clump volume. Asterisks denote significant difference in Bonferroni multiple comparison tests ($P = 0.05$). Abbreviation key: GASTROpod, OSTRAcod, AMPHIpod, ISOpod, DECApod, ECHINOderm.

TABLE 3.—Two-way fixed-effects ANOVA testing for differences in the total number of individuals among six prey categories (see Table 1) at two sites, one silted (No Name Key) and one unsilted (Burnt Point). Data were log transformed.

Source	df	SS	F	P
Site	1	0.841	18.78	0.001
Prey type	5	6.242	27.89	0.001
Site X prey type	5	0.847	3.78	0.006
Error	48	2.149		

(Marx and Herrnkind 1985b; Herrnkind and Butler 1986), 2) most spiny lobsters recovered from open sand were actually in corners, indicating edge-seeking behavior rather than selection for sand per se, and 3) only 10.6% of 142 spiny lobsters tested were found on sand even though it constituted 68% of the exposed substrate in aquaria. Silt had no effect on puerulus survival through metamorphosis to the first benthic instar (13% vs. 9% mortality in silted and unsilted algae, respectively), or time-to-metamorphosis (Fig. 3; $t = 0.37$, $P > 0.05$).

The total number of prey items consumed in the juvenile prey selection experiments ranged from 19 to 57 prey per lobster per 12 hours. Juveniles fed randomly from the three different prey combinations and frequencies offered to them (Table 1).

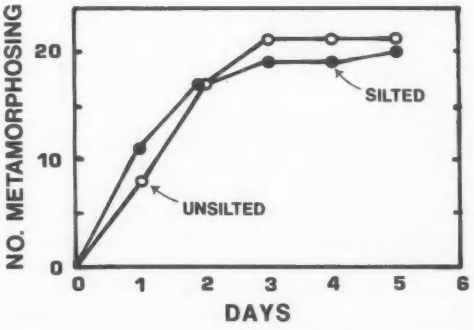

FIGURE 3.—Cumulative number of spiny lobster postlarvae metamorphosing as a function of time in one of two treatments: silted algae (*Laurencia* spp.) or unsilted algae. Twenty-three postlarvae were tested in each treatment; two postlarvae died in the unsilted treatment and three in the silted treatment.

DISCUSSION

The relative paucity of newly settled spiny lobsters in the heavily silted region around No Name Key over a 3-yr period indicates that low recruitment to benthic habitat is typical there. The absence of juveniles was apparently not due to a

lack of postlarval influx, which was higher than that at the unsilted Burnt Point site, but instead to low rates of postlarval settlement. Results from our habitat selection experiments support this hypothesis because settlement was significantly lower in silted algal clumps than in unsilted clumps. Previous studies showed that postlarvae selectively settled in highly architectured materials, like algal clumps (Herrnkind and Butler 1986). Thus, heavy silt covering an otherwise preferred habitat either masks the stimuli triggering settlement or contains stimuli that elicit rejection by pueruli. This question remains for further study. We cannot conclusively ascertain from our laboratory experiments the mechanisms governing habitat choice in the field where silted and unsilted habitats may not be adjacent, as they were in our aquaria. Yet for many species with planktonic larvae, these kinds of experiments, coupled with field observations of more general patterns of behavior and abundance, provide valuable insights into natural processes (Sulkin 1986).

Twenty percent of the pueruli we tested in laboratory tanks settled in silted clumps despite the general rejection of this habitat. Pueruli settling in silted algae probably metamorphose normally into the first benthic instar, as indicated by the equivalent time-to-metamorphosis and early postsettlement survival in both silt levels tested. However, subsequent residency by juveniles presumably is limited, given their great mobility and preference for unsilted algae with high food levels (Marx and Herrnkind 1985b; Herrnkind and Butler 1986). We found that prey abundances were significantly lower in silted algae. Thus, even if pueruli settle in the silted habitat the subsequent juveniles may leave to obtain adequate food. Frequent interclump movement by juvenile spiny lobsters, searching either for food or unsilted habitat, would predictably result in increased predatory mortality. Susceptibility to predation is much greater for juveniles in the open, than it is for individuals amidst algal clumps or dense seagrass (Herrnkind and Butler 1986). Thus, juvenile residency patterns and susceptibility to predation may, in addition to locally low settlement, contribute to the paucity of lobsters in the silted habitat.

The algal-bound silt load at No Name Key was roughly twice that at Burnt Point where spiny lobster recruitment was considerable. Our cursory surveys from Key Largo to Boca Chica Key indicate that similar silt levels are common, though geographically variable in Florida Bay. Benthic algae, including *Laurencia* spp., serve as sediment traps (Scoffin 1970) and demonstrate a remarkable resistance to siltation, growing profusely even in heavily silted areas. Silt in these areas is primarily calcareous, most of it probably a byproduct of sediment processing by deposit feeding shrimp (particularly *Callianassa*), annelids, and sea cucumbers.

We did not evaluate the geographic extent of siltation relative to spiny lobster settlement in Florida Bay. However, the demonstrated aversion to settling in naturally silted algae, characteristic of the region around No Name Key, strongly suggests that low postlarval recruitment and juvenile abundances would occur in similar conditions elsewhere. The sparse juvenile population at our silted site, one-tenth that of the unsilted site, suggests deleterious impact of high chronic silt levels in areas of potential recruitment. Human activities also cause siltation (Morton 1977; Allen and Hardy 1980). We noted that algal stands adjacent to heavily trafficked boat channels typically were more heavily silted than adjacent areas. We suspect the effect of manmade siltation to be similar to that from natural causes. Although it is now generally accepted that Florida Bay shallows serve as the main nursery grounds for the south Florida spiny lobster population (Marx 1986), the regional distribution of settlement and early juvenile habitation remains to be mapped. Future wide-area surveys by concerned researchers and agencies should include sampling of new spiny lobster recruits as well as silt levels. Meanwhile, sizable human activities such as channel construction, dredging, spoil dumping, coastal development, and mineral mining must be viewed as potentially deleterious to spiny lobster recruitment.

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LITERATURE CITED

ALLEN, K. D., AND J. W. HARDY.
1980. Impacts of navigational dredging on fish and wildlife: a literature review. U.S. Fish Wild. Serv., Biol. Serv. Program FWS/OBS-80/07, 81 p.

ALLER, R. C., AND R. E. DODGE.
1974. Animal-sediment relations in a tropical lagoon, Discovery Bay, Jamaica. J. Mar. Res. 32:209–232.

ANDREE, S. W.
1981. Locomotory activity patterns and food items of benthic postlarval spiny lobsters, *Panulirus argus*. MS Thesis, Florida State University, Tallahassee, FL, 50 p.

AZIZ, K. A., AND J. G. GREENWOOD.
1982. Response of juvenile *Metapenaeus bennettae* Racek & Doll 1975 (Decapoda: Penaeidae) to sediments of differing particle size. Crustaceana 43:121–126.

BOTERO, L., AND J. ATEMA.
1982. Behavior and substrate selection during larval settling in the lobster *Homarus americanus*. J. Crust. Biol. 2:59–69.

CALINSKI, M. D., AND W. G. LYONS.
1983. Swimming behavior of the puerulus of the spiny lobster *Panulirus argus* (Latrielle, 1804) (Crustacea: Palinuridae). J. Crust. Biol. 3:329–335.

CORTES, J. N., AND M. J. RISK.
1985. A reef under siltation stress: Cahuita, Costa Rica. Bull. Mar. Sci. 36:339–356.

CRISP, D. J.
1974. Factors influencing the settlement of marine invertebrate larvae. *In* P. T. Grant and A. M. Mackie (editor), Chemoreception in marine organisms, p. 177–265. Acad. Press, N.Y.
1976. Settlement responses in marine organisms. *In* R. C. Newell (editor), Adaptation to environment: essays on the physiology of marine animals, p. 83–124. Butterworths, Lond.

GRAY, J. S.
1974. Animal-sediment relationships. Oceanogr. Mar. Biol. Annu. Rev. 12:223–261.

HERRNKIND, W. F., AND M. J. BUTLER IV.
1986. Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus*. Mar. Ecol. Prog. Ser. 34:23–30.

HOWARD, A. E., AND D. B. BENNETT.
1979. The substrate preference and burrowing behavior of juvenile lobsters (*Homarus gammarus* (L.)). J. Nat. Hist. 13:433–438.

JOHNSON, D. H.
1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

JONES, G., AND S. CANDY.
1981. Effects of dredging on the macrobenthic infauna of Botany Bay. Aust. J. Mar. Freshwater Res. 32:379–398.

LITTLE, E. J.
1977. Observations on recruitment of postlarval spiny lobsters, *Panulirus argus*, to the South Florida coast. Fla. Mar. Res. Publ. No. 29, 35 p.

LITTLE, E. J., JR., AND G. R. MILANO.
1980. Techniques to monitor recruitment of postlarval spiny lobsters, *Panulirus argus*, to the Florida Keys. Fla. Mar. Res. Publ. No. 37, 16 p.

LYONS, W. G.
1980. Possible sources of Florida's spiny lobster population. Proc. Gulf Caribb. Fish. Inst. 33:253–266.

MARX, J. M.
1986. Recruitment and settlement of spiny lobster pueruli in south Florida. Can. J. Fish. Aquat. Sci. 43:2221–2227.

MARX, J. M., AND W. F. HERRNKIND.
1985a. Macroalgae (Rhodophyta: *Laurencia* spp.) as a habitat for young juvenile spiny lobsters, *Panulirus argus*. Bull. Mar. Sci. 36:423–431.
1985b. Factors regulating microhabitat use by young juvenile spiny lobsters, *Panulirus argus*: food and shelter. J. Crust. Biol. 5:650–657.

MORTON, J. W.
1977. Ecological effects of dredging and dredge spoil disposal: a literature review. U.S. Fish Wild. Serv. Tech. Pap. No. 94, Wash., D.C.

PEARSON, T. H., AND R. ROSENBERG.
1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Annu. Rev. 16:229–311.

POTTLE, R. A., AND R. W. ELNER.
1982. Substrate preference behavior of juvenile American lobsters, *Homarus americanus*, in gravel and silt-clay sediments. Can. J. Fish. Aquat. Sci. 39:928–932.

RHOADS, D. C.
1974. Organism-sediment relations on the muddy seafloor. Oceanogr. Mar. Biol. Annu. Rev. 12:263–300.

RHOADS, D. C., AND D. K. YOUNG.
1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. II. Reworking by *Molpadia oolitica* (Holothuroidea). J. Mar. Biol. 11:266–261.

ROACH, S. G.
1983. Survivorship, growth, and behavior of juvenile lobsters *Homarus americanus* Milne-Edwards in controlled environments in nature. Nova Scotia Dep. Fish. Mar. Res. Tech. Rep. Ser. 83-02, 60 p.

RUELLO, N. V.
1973. Burrowing, feeding, and spatial distribution of the school prawn *Metapenaeus macleayi* (Haowell) in the Hunter region (Australia). J. Exp. Mar. Biol. Ecol. 13:189–206.

SCOFFIN, T. P.
1970. The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. J. Sediment Petrol. 40:249–273.

SULKIN, S. D.
1986. Application of laboratory studies of larval behavior to fisheries problems. Can. J. Fish. Aquat. Sci. 11:2184–2188.

WITHAM, R., R. M. INGLE, AND H. W. SIMS JR.
1964. Notes on postlarvae of *Panulirus argus*. Q. J. Fla. Acad. Sci 27:289–297.

WITHAM, R., R. M. INGLE, AND E. A. JOYCE JR.
1968. Physiological and ecological studies of *Panulirus argus* from the St. Lucie estuary. FL Board Conserv. Tech. Ser. 53:1–31.

A LIMITED INFORMATION APPROACH FOR DETERMINING CAPITAL STOCK AND INVESTMENT IN A FISHERY[1]

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ABSTRACT

There have been few empirical studies on the level of capitalization and investment in fisheries because the necessary data are often inadequate. Specifically, data on capital stock and investment in a fishery are not routinely collected and compiled or are limited in scope. In this study, a method is provided for estimating the aggregate capital stock and investment in a fishery utilizing the available information. Data on acquisition and list prices and vessel characteristics for a sample of New England vessels are obtained. The data are then used to estimate an hedonic cost function which specifies the acquisition price as a function of vessel characteristics. The resultant equations are subsequently used, with information on vessel characteristics for all New England vessels, to estimate aggregate capital stock and investment. The results indicate that substantial investment occurred in the otter trawl and scallop dredge fisheries, particularly since the Magnuson Fisheries Conservation and Management Act. Moreover, the results demonstrate that the number and change in the number of vessels are inadequate indicators of the level of capital stock and investment in a fleet comprised of vessels with heterogeneous characteristics.

The common property nature of fisheries is recognized as causing excess capitalization and harvesting capacity (Gordon 1954). The theoretical argument is that since fishermen do not have to pay for the utilization of common property fish stocks, new vessels enter a fishery until net revenue is driven to zero. This common-property feature results in more capital and investment than is economically optimum. Public regulation of fishing industries is usually advocated to redress the excess entry, economic inefficiency, and loss of economic rents in a common property fishery (Scott 1979; Sissenwine and Kirkley 1982).

In essence, overcapitalization and excess investment are perceived to be the reasons for many of the major fisheries problems (Hilborn 1983). Economists argue that management of overcapitalization is necessary to realize the benefits of fisheries (Cunningham et al. 1985). Alternatively, gains from fisheries management require control of overcapitalization and excess investment (Charles 1983a, b).

Clark et al. (1979) and Charles (1983a, b) extended the static theory of optimal fisheries investment as developed by Gordon (1954). They also demonstrated the relationships between investment, capital stock, overexploitation, and fisheries management. They concluded that investment should be more conservative to prevent overexploitation.

The economic literature provides substantial justification for the need to solve the problems of overcapitalization and excess investment. Yet, few empirical studies document the level of capitalization and investment.[4] Moreover, there appears to be no attempt by any U.S. agency to routinely collect and compile statistics on either the stock of capital or the level of investment in U.S. fisheries. Overcapitalization and excess investment, though, continue to be suggested as the reasons for many of the economic problems of fisheries.

Since data are often inadequate, many empirical studies on fisheries consider capital stock and investment in terms of the number of vessels. That is, capital stock and investment in a fishery are tyically measured in terms of number of vessels. In the absence of appropriate information, the number of vessels may be the only basis for examining overcapitalization and excess investment. Alternatively, if a fleet has identical-sized vessels, fixed inputs or vessel characteristics, and

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[4]Tettey et al. (1986) provided an exception, but their analysis is restricted to the shrimp fishery and is based on cost data obtained from boat builders.

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gear, the number of vessels may be used to indicate the stock of capital and investment. However, Kendrick (1961) demonstrated that the total number of operating units, such as the number of plants, is an inadequate measure of capital stock. Also, few fleets have identical-sized vessels, characteristics, or gear. As a consequence, the number of vessels does not provide adequate information to indicate the level of capitalization and investment.

This study presents an approach for estimating the aggregate or industry level of capital stock and investment in a fishery comprised of heterogeneous vessels using available information. Data available include acquisition and list prices for some but not all vessels and boat characteristics for all vessels in a fleet. The approach was developed and used to obtain estimates of capital stock in support of the United States and Canadian maritime boundary dispute. It is viewed as an initial step towards examining the problems of excess capitalization by providing estimates of aggregate capital stock and investment.

THE DEFINITION AND MEASUREMENT OF CAPITAL AND INVESTMENT

Capital

The concept of capital has created problems for economists for quite some time. The term has been used in so many different contexts that it is a source of enormous confusion (Hirshleifer 1970). Sloan and Zurcher (1968), in their "Dictionary of Economics", define capital as "One of the major factors of production consisting of property from which an income is derived, expressed in terms of money. Popularly, the term is frequently used interchangeably with capital good. A distinction is sometimes made between money capital, or that part of the capital held in the form of money and bank deposits, and property capital, or that part of the capital held in the form of evidences of ownership such as stocks, bonds, and mortages."

Hirshleifer (1970) presented three meanings of capital: 1) real capital or capital stock, 2) capital value, and 3) liquid capital. Real capital is defined as a collection of capital goods or an aggregate of heterogeneous capital inputs. It is one of the major productive commodities or economic factors of production. Capital value is the net discounted value of expected future income streams associated with a capital good. Liquid capital is the level of current funds available or intended for investment.

In the case of fisheries, real capital or capital stock is the form of capital which should be examined with respect to the problems of overcapitalization and excess harvesting capacity. It is the relevant measure of capital goods used or available for production (National Academy of Sciences 1979). Moreover, capital stock is the concept of capital used to define and measure the services of capital inputs which are required to harvest fish; that is, it is the concept of capital required to define the economic production technology of a fishery. Thus, this study is concerned with the concept of real capital stock.[5]

The measurement of capital stock in a fishery, however, presents several problems. First, capital inputs are usually quite heterogeneous and cannot be easily aggregated without restrictive assumptions about the form of the catch equation or fishermen's behavior. Conceptually, it should be possible to combine all the different types of capital goods by weighting each type by its average compensation (i.e., the rental price). However, information at this level of detail is typically not available. Second, fisheries agencies, particularly in the United States, generally do not collect and compile information necessary to calculate capital stock and investment. Third, in order to compare changes in capital stock over time, the measure of capital stock must be converted to some base period value by deflation.

In empirical economic studies of traditional industries, the common practice is to measure the capital input or stock by converting the purchase or acquisition price or the book values of capital to base period values by the use of a price index (National Academy of Sciences 1979). Varian (1984) noted: "The usual procedure is to measure capital value and then deflate by a price index; in some sense, this should measure the level of capital stock." In this study, the acquisition price is used as the measure of the stock of capital or capital value; the real stock of capital is obtained by dividing the capital value by the producer price index for heavy machinery.

Investment

The definition and measurement of investment is more straightforward than is the definition and

[5]The market value of capital, acquisition price, and cost of capital are used interchangeably in this study.

measurement of capital. In simple terms, investment is the exchange of money for some form of property. Although there are several types of investment (Branson 1972), attention is restricted in this study to an examination of net investment (i_n) which is defined as the difference between the stock of capital in two periods of time (Baumol 1977). This is the same concept of investment examined by Tettey et al. (1986).

Replacement investment is another type of investment. The sum of replacement investment and net investment equals total investment. Replacement investment is measured by multiplying the rate of depreciation times the level of the capital stock. Replacement investment, however, is not estimated in this study since the method and rate of depreciation must be arbitrarily assumed.

METHOD OF ANALYSIS

The Hedonic Approach

While the definition and measurement of real capital stock and investment are conceptually straightforward, limited data and heterogeneous capital inputs complicate the measurement of capital stock and investment. In particular, data are usually only available for a small number of vessels which are often similar in their characteristics; these data are inadequate for calculating actual or observed capital stock and investment in a fishery. However, data are available on the acquisition price and characteristics of vessels which permits estimation of the stock of capital by an hedonic approach. In turn, estimates of capital stock from the hedonic approach can be used to estimate net investment in a fishery.

The hedonic approach hypothesizes that the price of a commodity is influenced by its characteristics (Rosen 1974). The hedonic price or characteristics function in market equilibrium reflects both the distribution of marginal rates of substitution over households and the distribution of marginal rates of transformation over firms. In effect, the hedonic hypothesis states that goods may be valued for their attributes and that implicit or hedonic prices exist as a function of the attributes.

Griliches (1971) estimated hedonic cost functions of U.S. automobiles using advertised or list prices and actual transaction prices. Griliches, however, was concerned with explaining quality differentials. Ladd and Martin (1976) examined prices and demands for input characteristics using a Neoclassical input characteristics model. Triplett (1986) estimated quality adjusted price indexes for computers. Thus, there is a history of deriving prices of commodities as a function of their characteristics.

The hedonic approach offers several attractive properties for estimating capital stock in fishing industries. First, the hedonic method incorporates changes in the quality of capital over time (Triplett 1986). This is because changes in quality should be reflected in vessel acquisition prices. The hedonic approach, thus, permits a quality adjusted measure of capital stock to be obtained. In contrast, vessel count ignores changes in the quality of capital. Second, the hedonic approach allows easy aggregation of the heterogeneous capital inputs frequently observed in a fishing fleet because the heterogeneous capital is measured by value rather than physical measures.

In the hedonic approach, cost (C) or input price may be expressed as a function of the associated characteristics of the commodity or input,

$$C = f(CH_1, CH_2, \ldots, CH_n) \ , \qquad (1)$$

where C is cost, CH_i is the ith characteristic (Braeutigam et al. 1982). The characteristic cost equation can be obtained either from a dual specification or by determining the reduced form equilibrium equation.

The Dual and Reduced Form

The dual specifies cost as a function of input prices and their characteristics. The partial derivative of the dual cost function with respect to input prices yields the demand for the inputs as a function of prices and input characteristics. The reduced form is obtained by solving structural equations, equations which explain the behavior and interrelations of endogeneous variables, of demand and supply for the endogeneous variable, price, in terms of exogeneous variables and disturbance terms.[6]

In this study, the reduced form is directly specified and estimated for two reasons: First, all of the input price data necessary for estimating a dual are not available. Second, estimation of the structural equations is complicated by the need to use a limited dependent variable method of estima-

[6]See Rosen (1974) for additional information on obtaining reduced form equations for hedonic prices.

tion since demand is a discrete choice, and there are individuals or firms which do not purchase a vessel.

Rather than attempt to deal with these difficulties which do not appear to have widely accepted solutions, it is assumed that there are underlying structural equations of demand and supply which permit the derivation of the reduced form equation. Moreover, the direct specification and estimation of the reduced form is the more commonly used approach to estimate the value of a commodity as a function of its characteristics (Bockstael et al. 1986). Last, the use of the reduced form should not create a problem since the hedonic function is a joint envelope in characteristic space of demander's bid schedules and sellers offer schedules, and thus, the observed implicit price locus is a reduced form equilibrium vector reflecting both supply and demand influences. As a result, shifts in both market demand and supply are incorporated into the reduced form equilibrium vector.

The Capital Stock Model

As previously indicated, it is common practice to use the acquisition price as a measure of capital stock. By the hedonic approach, the capital stock or acquisition price of a fishing vessel is postulated to be a function of several vessel characteristics. The following general specification is considered:

$$C = f(LN, CS, YEAR, FI, AGE, DNO, HPWR, GRT), \quad (2)$$

where C is the list or advertised price or the acquisition price of a vessel, LN is length, CS is hull type (1 = steel, 0 = other), FI is fishery or gear type,[7] AGE is age of vessel, DNO is a dummy variable for new and used vessels (DNO = 1 for new and 0 for used), HPWR is engine horsepower, and GRT is gross registered tonnage. The variable year equals the year of the observation. It is included to incorporate technological changes over time, such as the introduction of electronics and stern trawling, and structural changes in the industry such as changes in organization of capital and fish markets and changes in public regulation.

Functional Form

Several functional forms could be specified for Equation (2). Alternatively, generalized Box-Cox (Box and Cox 1962) transformations could be used to determine the functional form. However, the selection of functional form is mostly concerned with obtaining the relationship between the dependent variable and individual independent variables.This study is primarily concerned with estimating the capital stock. Moreover, it may be quite difficult to estimate capital stock from Box-Cox transformations or other functional forms since the conditional expectation is often of a complex form (Smallwood and Blaylock 1986). Also, Dadkhah (1984) noted that predictions based upon some transformations and functional forms result in biased predictions and asymmetric confidence intervals.

Since this study is primarily concerned with estimating capital stock and investment rather than estimating the implicit prices for characteristics, a linear functional form is proposed for Equation (2). The capital stock equation is specified as a second-order polynominal in order to provide an approximation to an unknown, underlying hedonic function. This is equivalent to specifying a generalized quadratic flexible functional form and imposing zero valued restrictions on the cross product coefficients or interaction terms (Lau 1978). Flexible functional forms are widely used in economic studies concerned with determining the underlying economic structure because they impose very little structure on the economic equations of concern (Blackorby et al. 1978).

Postulated Relations

The postulated relations between cost and each of the explanatory variables is as follows: 1) the coefficients for the first order terms of vessel tonnage, length, and engine horsepower should be positive since costs should increase as the size characteristics increase; 2) the coefficient for steel-hulled vessels should be positive since steel vessels are generally more expensive than wood or fiberglass vessels; 3) the dummy variable coef-

[7]Gear type is an integer valued variable set equal to the gear codes used by the Northeast Fisheries Center. This may influence the results similarly to the use of nonbinary dummy variables (Kmenta 1971). The use of this variable implies that the cost difference between gear types is equal to a scalar multiple of the lowest integer valued gear code. Thus, statistical rejection of cost differences due to gear type is actually a rejection of differences not being equal to scalar multiples. However, the large number of gear codes prohibits their separate treatment.

ficient for new vessels should be positive since new vessels tend to cost more because they are newer and usually incorporate more recent technological advances; 4) the second-order coefficients for the size characteristics are expected to be negative since cost is believed to increase at a decreasing rate in response to increases in the size of a vessel.

THE DATA

Data used to estimate the capital stock equation were obtained from three sources: First, information on vessel acquisition price and associated characteristics were obtained for 164 new vessels from the Northeast Regional Office of the National Marine Fisheries Service.[8] Second, data on list prices and vessel characteristics for 946 used vessels were obtained from various trade magazines and vessel brokers. Third, detailed vessel and fishery data were obtained from the U.S. Coast Guard master vessel listing and the Northeast Fisheries Center. Data were obtained for the years 1965 through 1981.

The first two sets of data were used to estimate the capital stock equations. The third data set was used to estimate aggregate capital stock and investment in selected New England fisheries using the estimated capital stock equations; that is, vessel characteristics for all of the vessels in the New England fleet were inserted into the estimated capital stock equations to obtain estimates of capital stocks per vessel in a given year. The estimated capital stock per vessel was summed over all vessels in a year to obtain total or aggregate capital stock. Net investment was then calculated as the annual change in total capital stock.

The use of both the list and acquisition prices, however, presents a problem. The list price reflects the supply price or the price at which a vessel is offered for sale. The acquisition price reflects the price determined by the equilibrium between demand and supply. As a consequence, estimates of capital stock and investment may be in error.

It is not known by how much the acquisition price differs from the list price for used vessels. Thus, the magnitude of the error cannot be calculated. Since the list price is not less than the acquisition price, estimates of capital stock based on Equation (2) are likely upwards biased. Counter to this problem is the argument that by the time a vessel is ready for fishing, required capital modifications or improvements may result in the capital stock being close in value to the list price.

There are no completely satisfactory economic justifications for using both the list and acquisition prices. Two possible justifications are that Griliches (1971) and others used both prices, and capital improvements or modifications may be nearly equal to the difference between the list and acquisition prices. Another possible justification is the accepted use of cost data obtained from boat builders as in Griffin et al. (1978) which may impose similar problems plus the statistical problem of measurement error. In the remainder of this paper, the term "acquisition price" is used although the estimation and calculation of capital stock and investment are based on both price series.

EMPIRICAL RESULTS

Equation (2) was estimated by ordinary-least-squares with the dependent variable, the acquisition price, measured in both nominal and real terms; the real price is the nominal price deflated by the producer price index for heavy machinery. As previously stated, deflation is necessary to estimate the real capital stock. The estimated coefficients and statistical results are presented in Tables 1 and 2.

Equation (2), however, was also estimated using data for several groups of years between 1965 and 1981. The reason for considering different time periods was that prior knowledge of New England fisheries suggested that various changes occurred in the fisheries during the selected time periods.[9] Moreover, economic studies of New England fisheries have often been criticized for assuming stable relationships over time or over different cross sectional units. Failure to incorporate changes in the estimated relationship between cost and vessel characteristics over time may result in biased parameter estimates.

Changes which have possible ramifications for the estimated relationships include 1) depressed resource conditions and the presence of foreign fishing between 1965 and 1971; 2) management by the International Commission for Northwest

[8]Data are confidential and may not be available to other researchers or the general public.

[9]Additional information on possible structural changes in New England fisheries is available in Kirkley et al. (1982), Dewar (1983), Doeringer et al. (1986), and Kirkley (1986).

TABLE 1.—Parameter estimates of

Years	N	Constant	GRT	GRT²	HPWR	HP
1965–71	133	13474.9	616.45	−5.25	−201.68	
		²(0.30)	(3.36)	(5.12)	(5.58)	(8.
1972–75	216	−489183.0	−316.47	8.64	52.61	−
		(4.72)	(2.23)	(10.49)	(1.03)	(1.
1976–77	164	−1755240.0	1,335.24	0.72	−60.09	
		(3.58)	(4.30)	(0.61)	(0.65)	(1.
1978–79	189	−3113870.0	673.62	−7.87	−116.75	
		(2.88)	(0.72)	(1.90)	(0.60)	(2.
1980	271	−188637.0	261.24	0.99	224.79	−
		(2.22)	(1.52)	(0.56)	(1.65)	(1.
1981	137	−50105.0	−4095.43	14.94	198.19	
		(1.25)	(2.28)	(2.09)	(1.60)	(1.
1965–81	1110	−528304.0	713.86	−0.22	−162.83	
		(7.04)	(2.05)	(2.15)	(1.57)	(5.

[1]Variables are defined as follows: 1) GRT and GRT² are gross registered tonnage a
its value squared; 2) HPWR and HPWR² are engine horsepower and its value squar
3) LN and LN² are vessel length and its value squared; 4) YEAR is the year of obser
tion; 5) DNO is a dummy variable for new and used vessels (1 = new, 0 = otherwis

TABLE 2.—Parameter estimates of he

Years	N	Constant	GRT	GRT²	HPWR	HP
1965–71	133	48304.1	724.35	−6.84	−219.74	
		²(1.01)	(3.74)	(6.33)	(5.76)	(8
1972–75	216	−81500.3	−185.96	5.18	32.62	−
		(1.17)	(1.96)	(9.37)	(1.05)	(1
1976–77	164	−782782.0	738.59	0.47	−31.06	
		(2.88)	(4.28)	(0.71)	(0.60)	(1
1978–79	189	−1024330.0	331.40	−3.76	−59.41	
		(2.02)	(0.75)	(1.94)	(0.65)	(2
1980	271	−78677.5	108.96	0.42	93.75	
		(2.22)	(1.52)	(0.57)	(1.45)	(1
1981	137	−18958.9	−1549.55	5.65	74.99	
		(1.25)	(2.28)	(2.09)	(1.60)	(1

[1]Variables are defined as follows: 1) GRT and GRT² are gross registered tonnage
its value squared; 2) HPWR and HPWR² are engine horsepower and its value squar
3) LN and LN² are vessel length and its value squared; 4) YEAR is the year of obse
tion; 5) DNO is a dummy variable for new and used vessels (1 = new, 0 = otherwi

ates of hedonic equation for nominal capital stock.

	Variables[1]								
	HPWR[2]	LN	LN[2]	YEAR	DNO	FI	CS	AGE	R^2
	0.51	−208.99	11.46	−20.0	15692.2	−294.2	2315	−660	0.93
	(8.54)	(0.48)	(2.89)	(0.03)	(1.89)	(1.38)	(0.84)	(3.35)	
	−0.13	6330.40	−59.33	4722.7	20176.7	−290.1	12117	−524	0.91
	(1.74)	(6.10)	(5.21)	(3.40)	(2.00)	(1.10)	(4.95)	(2.56)	
	0.16	6170.21	−56.79	20668.5	24038.5	968.7	12813	−749	0.85
	(1.65)	(4.24)	(4.04)	(3.17)	(1.82)	(1.96)	(3.07)	(1.83)	
	0.44	1449.86	44.53	38888.1	2232.4	−259.4	13897	−6693	0.84
	(2.06)	(0.50)	(2.02)	(2.81)	(0.91)	(0.19)	(1.82)	(8.15)	
	−0.05	6059.50	−10.82	—	22818.2	1110.8	3969	−5867	0.89
	(1.33)	(2.09)	(1.49)		(1.93)	(1.87)	(1.44)	(9.25)	
	0.21	8208.01	−2.72	—	10463.9	75.6	34225	−9323	0.78
	(1.65)	(2.06)	(0.05)		(1.87)	(1.39)	(1.74)	(7.20)	
	0.58	4054.12	−30.61	5967.9	45970.8	990.8	55730	−2217	0.82
	(5.25)	(2.47)	(2.28)	(6.20)	(3.59)	(1.42)	(4.60)	(4.08)	

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otherwise);

6) FI is a nonbinary dummy variable for gear type; 7) CS is a dummy variable for hull construction (1 = steel, 0 = otherwise); and 8) AGE is the age of the vessel.
[2]Numbers in parentheses are t-statistics.

s of hedonic equation for real capital stock, 1967 = 100.

	Variables[1]								
	HPWR[2]	LN	LN[2]	YEAR	DNO	FI	CS	AGE	R^2
4	0.54	−388.90	13.86	−500.2	18111.3	−273.8	2610	−653	0.89
	(8.72)	(0.85)	(3.28)	(0.73)	(1.97)	(1.21)	(0.90)	(3.15)	
2	−0.07	4009.60	−36.21	−117.8	13187.6	−213.9	8451	−411	0.90
	(1.61)	(5.75)	(4.73)	(0.13)	(1.94)	(1.21)	(5.15)	(3.00)	
6	0.08	3518.20	−32.20	8924.9	12827.3	559.8	11198	−422	0.83
	(1.18)	(4.35)	(4.13)	(2.46)	(1.98)	(2.04)	(3.11)	(1.95)	
1	0.21	897.93	19.14	12618.4	1074.3	−144.4	6882	−3147	0.81
	(2.16)	(0.66)	(1.85)	(1.95)	(0.09)	(0.23)	(2.60)	(8.16)	
5	0.02	2527.30	−4.51	—	9517.2	463.3	1655	−2447	0.89
	(1.33)	(2.09)	(1.49)		(1.94)	(1.87)	(1.44)	(9.25)	
9	0.08	3105.60	−1.03	—	3959.1	28.6	12949	−3527	0.78
	(1.65)	(2.06)	(0.05)		(1.87)	(1.39)	(1.74)	(7.20)	

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otherwise);

6) FI is a nonbinary dummy variable for gear type; 7) CS is a dummy variable for hull construction (1 = steel, 0 = otherwise); and 8) AGE is the age of the vessel.
[2]Numbers in parentheses are t-statistics.

Atlantic Fisheries and increased fuel prices between 1972 and 1975; 3) the formulation and implementation of the Fisheries Conservation and Management Act in 1976 and 1977; 4) extremely restrictive regulations in 1978 and 1979; and 5) a long dock strike in New Bedford, frozen harbors, and foreign purchases from American fishermen in 1981. In addition, there was substantial entry of new steel-hulled vessels between 1975 and 1977 and 1979 and 1980.

Chow (1960) tests of the equality of regression equations were conducted to further examine the possibility that the statistical relationships between cost and vessel characteristics changed over time. The Chow test is an F-test of the stability of the coefficients (Maddala 1977). The results of these tests are presented in Table 3.

The results of the tests indicate that the estimated relationships between cost and characteristics were not the same for the selected time periods. Alternatively, the hypothesis of the equality of the regression equations for different periods of time could not be accepted at any reasonable level of significance. However, these results only verify that different models should be estimated for different periods of time. They are not conclusive proof of the selection of the years for a particular group of years. A more accurate determination of the years to be included in each group requires considerably more estimation and hypothesis testing which is beyond the intent of this study.

As indicated by the t-statistics in Tables 1 and 2, the age of the vessel, whether or not the vessel is new or used, and the size characteristics appear to be the more statistically significant explanatory variables. These results are consistent with the results of Griffin et al. (1978). The statistically significant negative coefficients for the size characteristics during the years 1972–75 are particularly interesting. These years coincide with the Arab oil embargo when fuel prices increased; expected increases in future operational costs may have deterred new entry. The results also indicate that the value of a vessel declines as it becomes older. The coefficient for hull construction, CS, suggest that steel-hulled vessels are more expensive than are those of other materials such as fiberglass, ferro cement, wood, and aluminum. There does not appear to be a difference in the value of a vessel based on gear type. This may be a result of specification problems with the dummy variable for gear type (see footnote 7).

It is of further interest to examine the elasticities of cost with respect to the vessel characteristics.[10] These are presented in Table 4. As indicated, vessel tonnage, length, and age have the greatest influence on the acquisition price. The elasticity for length is consistent with the manner in which vessels are sold; that is, vessel prices are largely stated in terms of their length.

There are, however, inconsistences in the estimated capital stock equations and elasticities. In

TABLE 3.—Results of tests for the equality of regression equations.

Periods tested	F-statistic[2]	Critical values[1] 0.05	0.01
1965–71 1972–75 1976–77 1978–79 1980–81	39.38	$F_{12,1050} = 1.75$	$F_{12,1050} = 2.18$
1965–71 1972–75	8.45	$F_{12,325} = 1.75$	$F_{12,325} = 2.18$
1965–75 1976–81	20.55	$F_{12,1086} = 1.75$	$F_{12,1086} = 2.18$
1965–75 1976–79	21.33	$F_{12,668} = 1.75$	$F_{12,668} = 2.18$
1976–77 1978–79	3.60	$F_{12,329} = 1.75$	$F_{12,329} = 2.18$
1976–77 1978–81	3.22	$F_{12,737} = 1.75$	$F_{12,737} = 2.18$
1976–79 1980–81	3.35	$F_{12,737} = 1.75$	$F_{12,737} = 2.18$
1980 [3]1981	2.76	$F_{12,384} = 1.75$	$F_{12,384} = 2.18$

[1]F-statistic for denominator degrees of freedom equal to infinity.

[2]Restricted residual sum of squares obtained by pooling data over all time periods and estimating Equation (2). Unrestricted residual sum of squares obtained by estimating Equation (2) for each period being examined and then adding the residual sum of squares for each equation.

[3]Residual sum of squares obtained from estimating Equation (2) without the time variable.

[10] Elasticities indicate the percentage change in cost resulting from a 1% change in the value of a characteristic.

TABLE 4.—Estimated elasticities of cost with respect to vessel characteristics.[1]

Year	Elasticities GRT[2]	HPWR	LN	AGE
1965–71	0.43	0.06	2.88	−0.32
1972–75	0.78	−0.04	−0.08	−0.08
1976–77	1.14	0.09	0.11	−0.11
1978–79	−0.14	0.30	2.38	−0.40
1980	0.16	0.30	1.43	−0.30
1981	−0.64	0.56	2.38	−0.41

[1]Elasticities based on nominal estimates and observed mean values of cost and vessel characteristics.

[2]GRT is gross registered tonnage; HPWR is engine horsepower; LN is length; AGE is age of vessel.

particular, not all of the estimated coefficiencts have the desired or expected sign. For example, the coefficient for tonnage in the 1981 estimate is negative and that for the square of tonnage is positive. In contrast, a positive coefficient for tonnage was expected since vessel cost should increase with vessel tonnage, and the coefficient for tonnage squared was expected to be negative because vessel costs are believed to increase at a decreasing rate.

The incorrect signs could be the result of multicollinearity between vessel characteristics. Auxiliary regressions, though, do not indicate severe multicollinearity. The R^2 values are <0.35. If multicollinearity is a problem, its major effect is on the estimated relationships between cost and individual characteristics, the estimated elasticities, and the previously discussed Chow tests.

Multicollinearity is not thought to be a problem for several reasons. First, Chow tests in the presence of multicollinearity usually result in the acceptance of the null hypothesis of the equality of regression equations or that differences in the estimated coefficients are statistically insignificant (Maddala 1977). Second, multicollinearity does not pose a problem for estimating capital stock and investment; the estimated equations still permit estimation of the conditional mean.[11]

[11] For additional information on the problems of multicollinearity with respect to analysis and prediction, see Kmenta (1971).

The equations for the real or deflated value of capital were used to estimate total capital stock and investment for the New England fleet between 1965 and 1981. The real capital stock equations were applied to vessel data available from the Northeast Fisheries Center, and total capital stock was calculated as the sum of the stock over all vessels. Aggregate net investment was calculated as the difference in total capital stock between consecutive years.

Prior to estimating total capital stock and investment, it was necessary to define vessel type by gear to avoid double counting which might occur since vessels frequently switch port and gear. Three categories of gear types were established: 1) otter trawl, 2) scallop dredge, and 3) all others, which include lobster trawl and pots, herring gear, harpoons, etc. Vessels were assigned a gear type based on a plurality of days at sea. Estimates of capital stock and investment are presented in Table 5.

Several limitations should be considered when evaluating the estimates. First, there is the previously discussed problem that estimates of capital stock may be biased or overestimated. Second, estimates are only for New England vessels or those which are believed to be homeported in New England. Third, the capital stock and investment series pertain to New England and not the United States; that is, estimates should not be interpreted as net changes in the capital stock and investment in U.S. fisheries. Fourth, under-

TABLE 5.—Estimates of real capital stock and investment in New England harvesting sector, 1965–81.[1]

Year	Number of vessels	Capital stock			Investment			Index of investment
		Trawl	Dredge	Other	Trawl	Dredge	Other	
		$ Millions						
1965	594	25.96	16.29	1.98				
1966	619	28.84	14.75	2.82	2.88	−1.54	0.84	100
1967	628	39.37	11.42	1.63	10.53	−3.33	−1.19	276
1968	610	28.65	15.43	1.68	−10.72	4.01	0.05	−301
1969	602	29.22	12.92	1.29	0.57	−2.51	−0.39	−107
1970	607	25.61	8.29	1.37	−3.61	−4.63	0.08	−374
1971	620	23.65	12.80	1.47	−1.96	4.51	0.10	122
1972	655	27.01	7.74	4.70	3.36	−5.06	3.23	70
1973	666	28.42	7.12	5.13	1.42	−0.62	0.43	56
1974	695	21.26	4.19	6.40	−7.17	−2.93	1.27	−405
1975	737	29.04	5.15	8.48	7.78	0.96	2.08	496
1976	783	20.73	7.72	8.16	−8.31	2.57	−0.32	−278
1977	836	28.86	14.19	7.86	8.13	6.47	−0.30	656
1978	881	37.45	12.85	8.65	8.59	−1.34	0.79	369
1979	1,107	45.41	27.30	11.25	7.96	14.45	2.60	1147
1980	1,260	52.26	34.30	11.69	6.85	7.00	0.44	656
1981	1,246	43.35	30.15	11.60	−8.91	−4.15	−.09	−603

[1] Real investment and capital are deflated with producer price index for heavy machinery, 1967 = 100.

tonnage vessels or those which are <5 gross registered tons are excluded since data are unavailable; thus, total capital stock and investment in New England fisheries are underestimated.

Despite these limitations, the results provide information on investment and capital stock in New England fisheries which has not been available. As is characteristic of open-access fisheries, investment in New England fisheries appears to have increased over time. This is quite evident subsequent to the passage of the Magnuson Fisheries Conservation and Management Act of 1976. While possibly true, the observation that investment increased when the act was passed should not be construed to imply that the act was responsible for increased investment. Positive expectations regarding fish stocks or economic conditions could also be responsible for increases in capital stock and investment.

The largest increase in investment occurred in 1979 which coincided with the greatest influx of vessels. It also coincided with increased fish stocks in 1978 and 1979 and high vessel profits of the previous year. In 1979, 226 vessels entered the New England fisheries; 92 vessels were newly constructed.

Disinvestment also occurred, but the reasons are unknown.[12] Disinvestment may be associated with vessel sinkings, foreclosures on vessel mortgages, and exit from the region. Alternatively, if vessel prices reflect the expected net discounted present value of earnings from a fishery, the disinvestment or even changes in investment may be due to changes in economic expectations. Disinvestment occurred between 1968 and 1970, 1974, 1976, and in 1981.

Disinvestment between 1968 and 1970 may reflect expectations of declining future earnings. Disinvestment in 1974 may reflect the effects of high fuel prices. Disinvestment in 1976 and 1981 may be associated with fishermen's expectations of declining fish stocks, the effects of management, and high fuel prices.

The reasons for investment are also unknown. Increasing levels of investment between 1977 and 1980 may be due to economic expectations associated with fisheries management, fish stocks, and future earnings.

The real capital stock increased approximately 6% per year between 1965 and 1981. The largest increase occurred in 1978 and 1979 when there was a substantial increase in the number of new steel-hulled vessels and entry of vessels from the mid-Atlantic region. Capital stock declined in 1981 when some of the mid-Atlantic vessels left New England and the stocks of fish, particularly sea scallops, declined (Northeast Fisheries Center 1985).

The results also indicate why a vessel count should not be used to indicate capital stock or investment. The number of vessels increased between 1969 and 1970 and 1975 and 1976, but investment decreased in 1970 and 1976 (Table 6). Alternatively, the number of vessels increased in each year relative to 1965, but the real capital stock between 1969 and 1976 declined with respect to 1965.

TABLE 6.—Indices of capital stock based on constant dollar value and vessel count.

	Capital stock					
	Constant dollar value			Vessel count		
Year	Trawler[1]	Dredge[1]	Total	Trawler[1]	Dredge[1]	Total
1965	100	100	100	100	100	100
1966	111	91	105	102	94	104
1967	152	70	119	109	77	106
1968	110	95	103	104	106	103
1969	113	79	98	104	106	101
1970	99	51	80	108	74	102
1971	91	79	86	108	83	104
1972	104	48	89	108	74	110
1973	109	44	92	105	79	112
1974	82	26	72	107	49	117
1975	112	32	96	105	66	124
1976	80	47	83	109	202	132
1977	111	87	115	107	202	141
1978	144	79	133	116	189	148
1979	175	168	190	137	313	186
1980	201	211	222	158	440	212
1981	167	185	192	158	413	210

[1]Gear type assigned by plurality of days absent.

The inadequacy of using vessel count is more pronounced when comparing the indices based on gear type. As shown in Table 6, the number of trawl vessels in every year exceeded the number of vessels in 1965 while capital stock was less than that of 1965 for four years. The two scallop dredge indices also indicate dissimilar changes between vessel count and real capital stock. It may, though, be possible than an index based on vessel count and weighted by vessel size would more closely compare to the real capital stock index. The construction of these indices would require considerable additional analysis and determination of the weights necessary for aggregation.

[12]Hirshleifer (1970) provided additional information about disinvestment.

SUMMARY AND CONCLUSIONS

This study developed procedures for estimating the capital stock and net investment using only the information generally available. That is, data on acquisition and list prices for some but not all vessels and characteristics for most vessels in a fleet were used to estimate capital stock and investment in a fishery. An hedonic approach which specified the acquisition price as a function of vessel characteristics was suggested as a possible method for obtaining information necessary for estimating capital stock and net investment. It was argued that the approach was consistent with procedures used by economists to estimate the capital stock and investment in traditional industries.

Estimates were based on 1,110 observations obtained from NMFS and classified advertisements for the period 1965–81. Vessel characteristics pertaining to size and age were shown to be the more significant characteristics for explaining the value of a vessel. The corresponding information was then used to estimate the capital stock and investment in the New England fisheries.

An interesting result was that although investment increased over time, there also was disinvestment in the fisheries. It was suggested that this was possibly the result of vessel sinkings, exit of vessels from the region, foreclosures, and expectations of declining future net returns.

It also was demonstrated that a vessel count should not be used to indicate capital stock or investment. The number of vessels generally increased over time, but the level of capital stock did not coincide with these changes. This suggests that more attention should be given to developing economic measures of capital stock and investment.

A question still in need of attention, however, cannot be answered from this study. That is, given the level of investment, can an optimal utilization and allocation of resources be determined. The answer is clearly no. This requires management authorities to specify the objectives of fisheries management and a detailed bioeconomic model.

There is a need for more research on investment, and in particular, the determination of the optimum rate of investment. This includes research on the social discount rate, reasons for investment, and the marginal productivity of capital. More important, additional research is required to better address the issues of fisheries management, particularly whether or not public expenditures should be allocated to managing fisheries.

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LITERATURE CITED

BAUMOL, W. J.
1977. Economic theory and operations analysis. Prentice-Hall, Englewood Cliffs, N.J.

BLACKORBY, D., D. PRIMONT, AND R. R. RUSSEL.
1978. Duality, separability, and functional structure: theory and economic applications. North-Holland Publishing Company, Amsterdam.

BOCKSTAEL, N. E., W. M. HANNEMANN, AND I. E. STRAND.
1986. Measuring the benefits of water quality improvements using recreation demand models. Volume II of benefit analysis using indirect or imputed market methods. EPA contract No. CR-811043-01-0. U.S. Environmental Protection Agency, Washington, D.C.

BOX, G. E. P., AND D. R. COX.
1962. An analysis of transformations (with discussion). J. R. Stat. Soc., Ser. B:211–243.

BRAEUTIGAM, R. R., A. F. DAUGHETY, AND M. A. TURNQUIST.
1982. The estimation of a hybrid cost function for a railroad firm. Rev. Econ. Stat. 64:394–404.

BRANSON, W. H.
1972. Macroeconomic theory and policy. Harper & Row, Publishers, N.Y.

CHARLES, A. T.
1983a. Optimal fisheries investment:comparative dynamics for a deterministic seasonal fishery. Can. J. Fish. Aquat. Sci. 40:2069–2079.
1983b. Optimal fisheries investment under uncertainty. Can. J. Fish. Aquat. Sci. 40:2080–2091.

CHOW, G. C.
1960. Tests of equality between subsets of coefficients in two linear regressions. Econometrica 28:591–607.

CLARK, C. W., F. H. CLARKE, AND G. R. MUNRO.
1979. The optimal exploitation of renewable resource stocks: problems of irreversible investment. Econometrica 47:25–47.

CUNNINGHAM, S., M. R. DUNN, AND D. WHITMARSH.
1985. Fisheries Economics: an introduction. St. Martin's Press, N.Y.

DADKHAH, K. M.
1984. Confidence interval predictions from a logarithmic model. Rev. Econ. Stat. 66:527–528.

DEWAR, M. E.
1983. Industry in trouble: the Federal government and

New England fisheries. Temple University Press, Philadelphia, PA.

DOERINGER, P. B., P. I. MOSS, AND D. G. TERKLA.
1986. The New England fishing economy. The University of Massachusetts Press, Amherst, MA.

GORDON, H. S.
1954. The economic theory of a common property resource: the fishery. J. Polit. Econ. 62:124–142.

GRIFFIN, W. L., J. P. NICHOLS, R. G. ANDERSON, J. E. BUCKNER, AND C. M. ADAMS.
1978. Costs and returns data: Texas shrimp trawlers, Gulf of Mexico 1974–75. Texas A&M Univ., Dep. Agric. Econ. tech. Rep. TAMU-SG-76-601.

GRILICHES, Z.
1971. Hedonic price indexes for automobiles: an econometric analysis of quality changes. *In* Price indexes and quality changes, p. 103–130. Harvard University Press, Cambridge, MA.

HILBORN, R.
1985. Fleet dynamics and individual variation: why some people catch more fish than others. Can. J. Fish. Aquat. Sci. 32:2–13.

HIRSHLEIFER, J.
1970. Investment, interest and capital. Prentice-Hall, Englewood Cliffs, NJ.

KENDRICK, J.
1961. Some theoretical issues in capital measurement. Am. Econ. Rev. 51(2):102–111.

KMENTA, J.
1971. Elements of econometrics. Macmilliam Publishing Co., Inc., N.Y.

KIRKLEY, J. E., M. P. PENNINGTON, AND B. E. BROWN.
1982. A short-term approach for analyzing the effects of harvesting quotas. J. Cons. int. Explor. Mer 40:173–175.

KIRKLEY, J. E.
1986. The relationship between management and the technology in a multi-species fishery. Ph.D. Thesis, Univ. Maryland, Collage Park, MD.

LADD, G. W., AND M. B. MARTIN.
1976. Prices and demands for input characteristics. Am. J. Agric. Econ. 58:21–30.

LAU, L. J.
1978. Applications of profit functions. *In* M. Fuss and D. McFadden (editor), Production economics: a dual approach to theory and applications, p. 133–216. North-Holland Publishing Company, Amsterdam.

MADDALA, G. S.
1977. Econometrics. McGraw-Hill Book Company, N.Y.

NATIONAL ACADEMY OF SCIENCES.
1979. Measurement and interpretation of productivity. National Research Council, Washington, D.C.

NORTHEAST FISHERIES CENTER.
1985. Status of the fishery resources off the northeastern United States for 1985. U.S Dep. Commer., NOAA Tech. Memo. NMFS-F/NEC-42, 137 p. Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA.

ROSEN, S.
1974. Hedonic Prices and implicit markets:product differentiation in pure competition. J. Polit. Econ. 82:34–55.

SCOTT, A.
1979. Development of economic theory of fisheries regulation. J. Fish. Res. Board Can. 36:725–741.

SISSENWINE, M. P., AND J. E. KIRKLEY.
1982. Fishery management techniques:practical aspects and limitations. Mar. Policy 6:22–42.

SLOAN, H. S., AND A. J. ZURCHER.
1968. Dictionary of economics. Barnes & Noble, Inc., N.Y.

SMALLWOOD, D. M., AND J. R. BLAYLOCK.
1986. Forecasting performance of models using the Box-Cox transformation. Agric. Econ. Res. 38:14–24.

TETTEY, E. O., W. L. GRIFFIN, J. B. PENSON, AND J. R. STOLL.
1986. Implications of tax policy on investment in a common property resource. N. Am. J. Fish. Manage. 6:100–104.

TRIPLETT, J.
1986. The economic interpretation of hedonic methods. Surv. Curr. Bus. 66:36–40.

VARIAN, H. R.
1984. Microeconomic analysis. 2d, ed. W. W. Norton & Company, N.Y.

ANALYSES OF THE RELATIONSHIP BETWEEN THE DISTRIBUTION OF SEARCHING EFFORT, TUNA CATCHES, AND DOLPHIN SIGHTINGS WITHIN INDIVIDUAL PURSE SEINE CRUISES

Tom Polacheck[1]

ABSTRACT

The fine scale distribution of searching effort within individual purse seine cruises in the eastern tropical Pacific is analyzed in relationship to sightings of spotted dolphin, *Stenella attenuata*, and tuna catches. The data for these analyses were derived from detailed observations made by National Marine Fisheries Service observers aboard U.S. purse seiners. A clustering algorithm is developed which separates the activity of a vessel into areas where sets were common and areas where they are infrequent. Within clusters of high set densities, vessels tend to concentrate their searching effort. Vessels searched proportionately greater distances relative to the physical distances between sets while within clusters than when outside clusters. Encounter rates with schools of spotted dolphins tend to be either much higher or much lower within defined clusters than outside them. Clusters with low encounter rates were clusters in which non-dolphin associated tuna sets predominated. Because of this dichotomy in the magnitude of the dolphin encounter rates within clusters, overall encounter rates appeared to have relatively small biases if the concentration of searching effort within clusters is ignored. The average catch of tuna per set was higher within the defined clusters than between them. The overall results suggest that fine scale geographic effects need to be considered when using data from purse seiners to examine changes in relative abundances of either dolphins or tuna.

Catch and effort data underlie most indices of abundances used for assessing the status of commercially exploited fish stocks. The validity of using catch and effort data from commercial harvests has long been questioned because of the likelihood that fishermen concentrate their effort in areas of high fish densities (Helland-Hansen 1909). Yet, almost nothing is known about the allocation of effort by individual vessels. If data are available on the activity of individual vessels, these data have been mainly used for standardization of effort. The catch and effort activities within individual cruises have not been examined in detail (in part because the data for such an examination generally do not exist). The purpose of the present paper is to examine the searching behavior of tuna purse seiners in the eastern tropical Pacific (ETP) based on detailed data compiled by the National Marine Fisheries Service (NMFS). The main questions addressed are whether seiners concentrate their effort and what is the relation between searching behavior, encounter rates for dolphins, and tuna catches.

The maximization of profit is presumably a strong influence on the behavior of commercial fishermen. Upon leaving port, the catch rate realized by a fisherman is probably the most important factor affecting his profits. Given this orientation, it is reasonable to assume that fishermen have developed strategies of when and where to fish that increase their catch rates beyond that achieved by random search. There is little empirical information to support this assumption other than correlations, which have been noted for some fisheries, between the spatial distribution of catch rates and effort for the fleet as a whole (Gulland 1955; Calkins 1963).

In a fishery where the detection of fish depends upon visual cues, searching would be expected to be located in the vicinity of previously located fish, if there is a tendency for the underlying population to be spatially clustered. The search path for a vessel in such a fishery might be expected to look something like the hypothetical one depicted in Figure 1. The amount of crisscrossing or zigzagging in the vicinity of a catch and the area over which the search extends would be expected to vary between fishermen. The solution to the optimal searching strategy for such a situation is nontrivial and depends upon information on the

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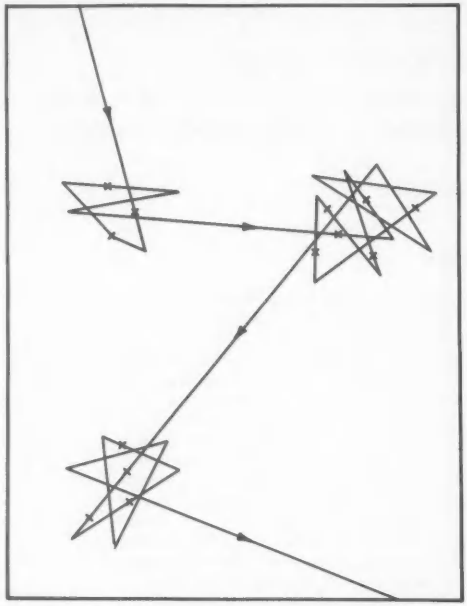

FIGURE 1.—A hypothetical cruise track for a vessel searching for clustered prey. The location of catches are indicated by ×s.

underlying distribution of the fish population (Koopman 1980). The question of optimal searching strategies for fishermen has been receiving increased attention (Pazynich 1966; Salia and Flowers 1979; Clark and Mangel 1983). These studies are primarily theoretical at this time and their application to actual fisheries requires knowledge of the spatial distribution of the fish population.

Locating schools of tuna (e.g., yellowfin, *Thunnus albacares*, and skipjack, *Katsuwonus pelamis*) in the purse seine fishery in the ETP depends on visual cues. Fishermen use a variety of cues including birds which feed on the same prey as tuna, disturbances on the surface of the water, floating debris which frequently have associated tuna, and schools of dolphins which are often associated with tuna (primarily yellowfin). Fishermen have names for the different types of sets depending upon what is associated with the tuna school. They refer to sets associated with floating debris as log sets, sets associated with dolphins as porpoise sets, and sets not associated with other animals (except possibly birds) as school sets. Fishermen when not engaged in a set usually spend their day actively searching for signs of tuna. They use 25× binoculars to scan the water while the boat cruises at speeds generally between 10 and 12 knots.

The distribution of schools of tuna, as well as schools of the most commonly associated dolphins (i.e., the spotted dolphin, *Stenella attenuata*), appears to be spatially and temporally clustered within the ETP considered as a whole (Calkins and Chatwin 1967, 1971; Blackburn and Williams 1975; Suzuki et al. 1978; Au et al. 1979[2]; Polacheck 1983). At finer geographic scales, there is little available information although Au et al. (fn. 2) suggested that schools of spotted dolphin tend to be locally concentrated in areas of convergences and fronts.

Given the above observation, it is not surprising that the detection or encounter process for tuna or dolphins does not, in general conform to a Poisson process when the distribution of searching times, searching distances, or physical distances between nearest encounters are analyzed (Polacheck 1983; Allen and Punsely 1984). In such analyses it is impossible to separate or distinguish the effects of nonrandom search from nonrandom distributions of tuna or dolphins.

In the harvesting of tuna schools associated with dolphins, fishermen chase and capture the associated dolphins (Perrin 1968, 1969), and some dolphins may be incidently killed. NMFS, as part of its responsibility under the Marine Mammal Protection Act of 1972 for managing and monitoring the status of dolphin populations, placed trained observers aboard tuna purse seiners. From the data collected by these observers, approximate cruise tracks can be drawn by connecting all positions that were recorded. Many of these approximate cruise tracks (e.g., Figure 2) have superficially a strong similarity to the hypothetical one depicted in Figure 1. It was this similarity that provided the impetus for the analyses presented below.

METHODS

NMFS observers aboard tuna purse seiners collected a wide variety of information, both on the sightings of marine mammals and fishing opera-

[2]Au, D. W. K., W. L. Peryman, and W. F. Perrin. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Natl. Mar. Fish. Serv., Southwest Fish. Cent., Adm. Rep. LJ-79-43, 59 p.

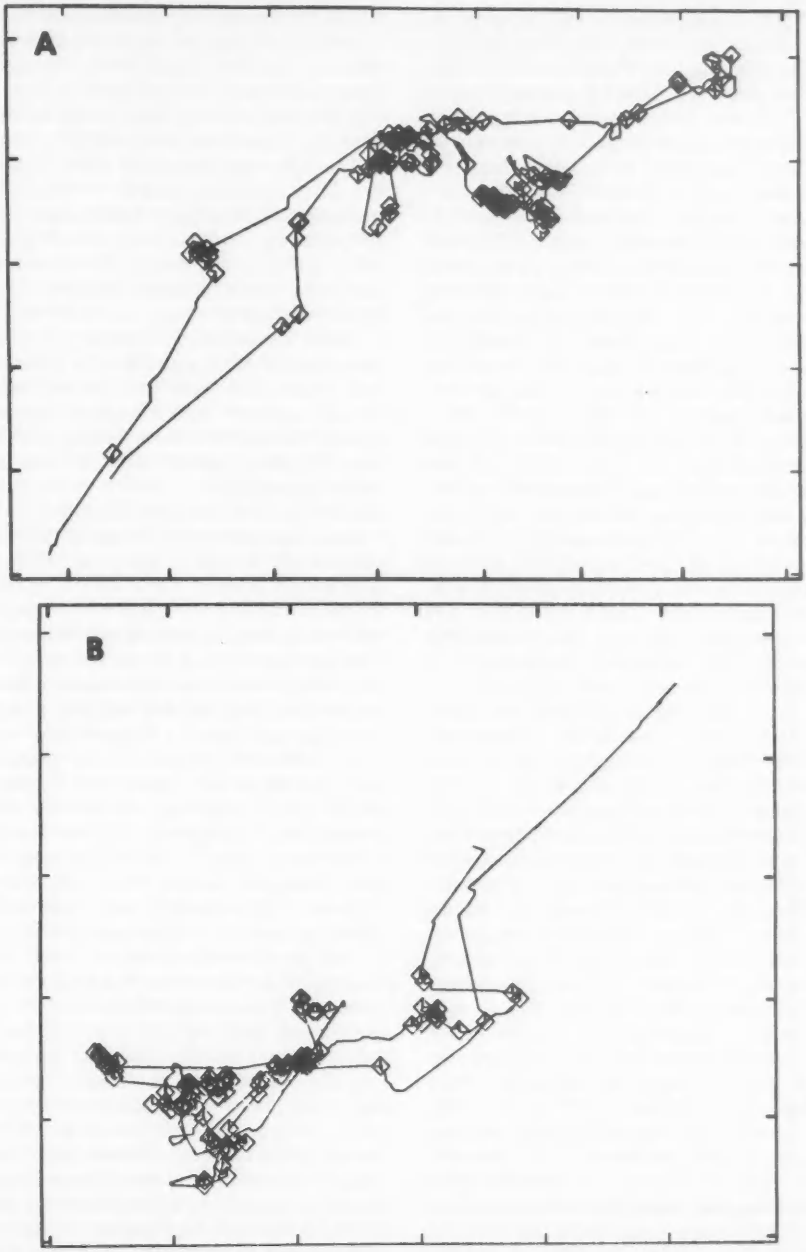

FIGURE 2.—Examples of the approximate cruise track for two tuna purse seiners. Diamonds represent the location of a set or chase. No geographic coordinates are given, and the orientation of figures were rotated at random so as not to compromise any proprietary fishing information. The distance between tick marks equals 300 nautical miles.

tions. Included in the recorded data are information on all changes in a vessel's activity; the location, type, and catch of all purse seine sets; and the location and identity of all marine mammal sightings. In these data, a vessel's activity is classified into one of five mutually exclusive categories: searching, running, setting, chasing, or resting. Searching is defined to be whenever a vessel is moving and the crew are actively searching for signs of tuna; running, anytime the vessel is moving but not actively searching for signs of fish (e.g., moving locations at night); chasing, anytime schools of dolphins are being pursued before the net has begun to be set. More detailed descriptions of the available data, collection procedures and their preparation for the analyses below can be found in Polacheck (1983, 1984[3]). The analyses in this paper were part of a larger project on the use of these observer data for assessing the relative abundances of dolphin stocks. As such, the emphasis in this paper is on the encounter rate for the most important dolphin species for the fishery (spotted dolphin), although catch rates for tuna are also considered. The results presented in this paper are based on two different approaches for analyzing the data. The first method is a set of nearest neighbor calculations, and the second is a cluster analysis.

The nearest neighbor calculations were performed in order to get an indication whether vessels tend to search in the vicinity of a previous encounter (either a sighting of marine mammals or a set on tuna). In these calculations, the physical distance between either the next or preceding encounter is compared with the distance to the nearest other encounter made within the entire cruise. Also, the proportion of times in which the nearest encounter is not either the next or preceding one is calculated. For a vessel that never returned to the area of an encounter, this proportion would equal 1. Similarly, if a vessel never returned to the area of an encounter, the ratio of the distance between either the next or preceding encounter and the distance to the nearest other encounter within an entire cruise would also equal 1. Note that the expected values for these proportions with random search are not necessarily 1. The expected value will be dependent both on the distribution of potential encounters and the definition of random search (see Discussion). These calculations were performed separately for sets and chases for tuna and for the sightings of spotted dolphin. In performing these nearest neighbor calculations, the first and last encounter during a cruise were not included.

The other main approach used for examining the data is a form of cluster analysis. When the sequences of distances between sets and chases within any cruise were examined, they appeared to be spatially and temporally clustered in the sense that sets and chases in which the distance to the next set or chase was small tended to be clumped sequentially. This observation led to the development of an algorithm for clustering sets and chases that were spatially and temporally related. Standard clustering algorithms were not appropriate in this situation because of the problem of scaling spatial and temporal distances within a common metric (i.e., how much time should be equal to a given distance).

Note that the term "clustered" or "clustered distribution" is used in this paper to refer to any distribution in which high- and low-density areas are more frequent than would be expected if the distribution was generated by a Poisson process. The term is not meant to refer to any particular nonhomogeneous process. A cluster is considered as an area of high density and should not be construed as referring to a discrete unit.

The primary purpose of the clustering algorithm was to define areas which a fisherman might have thought to have a high density of potential fishing targets so that the searching behavior of a vessel could be compared between these areas and outside them. This analysis exploits the fact that the physical distance between events is partially independent of the distance that a vessel travels to locate them. Since the purpose of the algorithm was to define areas of potentially good fishing, chases of dolphin, as well as sets, have been included as events in the clustering algorithm. (Sets made for the purpose of washing the net were not used.) The clustering algorithm began with consideration of the distance between the first and second set and/or chase. If this distance was less than a specified amount, then these two events were placed in the same cluster, and the distance between these two and the third event were examined. This specified amount will be referred to as the clustering parameter. If the distance between the third event and either of the events within the cluster was less than the value of the clustering parame-

[3]Polacheck, T. 1984. Documentation of the time sequential files created from the tuna boat observer data bases for analyzing relative abundances. Natl. Mar. Fish. Serv., Southwest Fish. Cent., Adm. Rep. LJ-84-33, 26 p.

ter, this third event was included in the cluster and the fourth event was examined. Whenever a set or chase was found for which the distance between it and all members of the last defined cluster exceeded the clustering parameter, a new cluster was formed. This process was repeated until all sets and chases within a cruise were placed in a cluster.

Using this algorithm, all the activities within a cruise could be considered to occur either between or within clusters. Isolated sets or chases (i.e., clusters containing only a single event) were considered as occurring between clusters. Distances travelled (i.e., distance searched and distance run) within a cluster were defined as the distances travelled after the first set or chase until the last set or chase in that cluster. Distances travelled between clusters were defined from the last event of the previous cluster to the first event of the subsequent cluster. The distances travelled until the location of the first set or chase and after the last one were not included because of the large distances involved in reaching the fishing grounds.

The location of a cluster was estimated by calculating the centroid for all sets and chases within it. The size of a cluster was estimated by determining the radius of the smallest circle with a center at the centroid that encompassed all sets and chases within it.

The sensitivity of this algorithm to the value of the clustering parameter was examined for values of 50, 75, 100, and 150 miles. For most of the results, only clusters with at least three members are considered as clusters. Clusters with only two members have been excluded from most of the summary results describing a cluster and also in the comparisons of results between and within clusters. This was done because two physically close events did not seem to warrant being called a cluster. Yet, given the relative difficulty in locating potential sets, two close events might be considered as areas of potentially good fishing. Clusters with only two members contained 18% of all sets and chases when the cluster parameter equalled 50 miles and 6% of all sets when the value equalled 150 miles. The overall results and conclusions are robust to whether or not clusters with two members are included or excluded.

An average intercluster distance for a cruise was calculated in order to get an indication of the stability of the clustering algorithm to the value of cluster parameters. The intercluster distance was defined as the distance from the nearest member of a cluster or isolated set to the next set and represents the minimum value that the cluster parameter would have to be for a cluster or isolated set to be combined in a single cluster with the next set.

Encounter rates for schools of spotted dolphin for each cruise were calculated between and within clusters as the total number of sightings divided by the total distance searched. In these rates, if the first chase or set within a cluster was based on a sighting of spotted dolphin, this sighting was included in the encounter rates between and not within a cluster. For the analysis of these encounter rates, clusters were classified according to the percentage of the total number of sets and chases within a cluster that involved schools of dolphins. In calculating the number of events that occurred within a cluster, sequential non-dolphin sets in which no searching was done between them were counted as a single event. This was done to reduce the effect of multiple sets on the same floating object counting as a large cluster.

In order to see whether the searching behavior within the defined clusters resulted in biased estimates of encounter rates for dolphins if the clusters were ignored in the estimates, two different estimates for the overall encounter rate for a cruise were calculated and compared. The first estimate, which will be referred to as the unadjusted rate, was simply the total number of encounters divided by the total distance searched for an entire cruise. This would be an unbiased estimate if search was in fact random. The second estimate, which will be referred to as the adjusted encounter rate, was calculated as the weighted average of the encounter rate within and between clusters. The weights for the encounter rate within clusters were equal to the diameter of the cluster. The weights between clusters equalled the total distance searched between clusters. In effect, this adjusted encounter rate is an estimate of what the encounter rate would have been if a vessel had made a straight line crossing of each cluster. (In the calculation of these adjusted encounter rates, clusters with two members were treated the same as other clusters to simplify the calculations.)

The analyses in this paper are based on 35 cruises. This represents a subset of the cruises in 1979 with NMFS observers, which in turn is a subset of all purse seine cruises for tuna in the ETP during 1979. Analyses were restricted to 1979 because only for this year have the data

been carefully edited for positional errors. Cruises from 1979 were excluded either because of insufficient positional data or because the vessel made port stops during the middle of the cruise. Inclusion of the time spent searching on the way in and out of port could distort the results on searching and encounter rates between clusters. Preliminary analyses suggested that there is little difference in the results between vessels that went into port and those that did not. However, to avoid further complicating the analyses, these cruises have not been included (see Polacheck 1983 for more detail).

RESULTS

Is Effort Concentrated?

The percentage of sets or chases for which the nearest one was not the preceding or next set or chase ranged from 12 to 77 among cruises (Fig. 3). The mean percentage was 41 (SE = 1.9, n = 35). The average ratio of the physical distances between the next or preceding set or chase compared to the distance to the nearest set or chase within a cruise was 1.45 (SE = 0.044, n = 35) and ranged from 1.00 to 2.24. Consideration of the same statistics for the distances between sightings of spotted dolphin indicates an even more concentrated pattern. The mean percentage of sightings for which their nearest neighbor was not either the next or preceding one equalled 80 (SE = 2.8, n = 34, note one cruise recorded no sightings of spotted dolphins) and ranged from 25 to 100 (Fig. 4). The average ratio of the distance between the next or preceding sighting compared with the nearest sighting was 4.05 (SE = 0.261, n = 34) and ranged from 1.14 to 7.82. For these sighting statistics, low percentages and ratios near 1.00 are found in vessels with few sightings (Fig. 4). These results suggest that in general vessels return to the area of a previous sighting and/or set and search in that area at least 41% of the time.

There appears to be large differences among vessels in their ability and success at locating potential fishing targets. Thus, the average distance searched between sets or chases varies by about a factor of 4 among cruises, while the average physical distance between sets or chases varies by about a factor of 6 (Fig. 5). There is little relationship between the average distance searched between sets and chases and the average distance to the next one. However, vessels

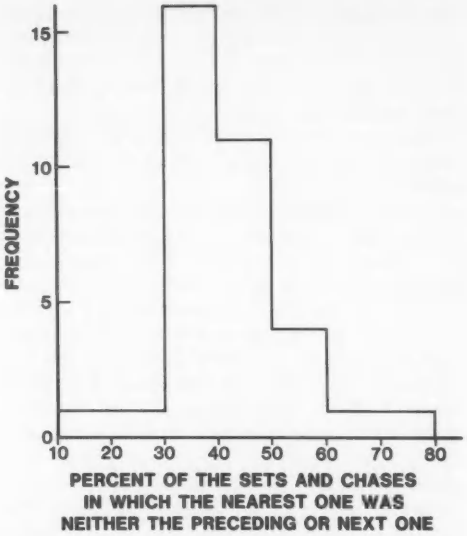

FIGURE 3.—The frequency distribution for the percentage of the sets and chases within a cruise for which the nearest other set or chase was neither the preceding or next one.

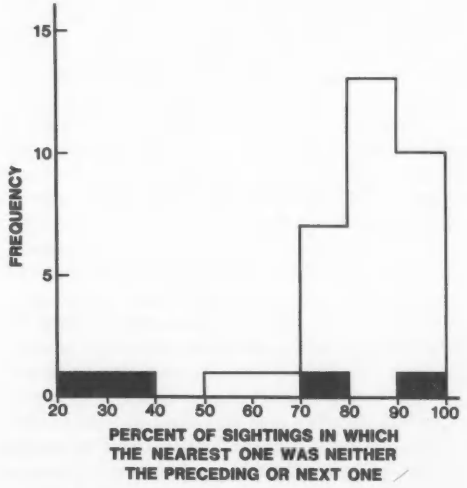

FIGURE 4.—The frequency distribution for the percentage of sightings of schools of spotted dolphins, *Stennella attenuata*, within a cruise for which the nearest other sighting was neither the preceding or next one. Shaded portions represent cruises with less than 15 sightings (note one cruise had no sightings of spotted dolphins).

with the largest distances between sets also have large average search distances, but the converse is not true (Fig. 5). The importance of dolphin fishing as compared to log and school fishing appears not to be related to these differences among cruises (Fig 6). It should be noted that the points in Figure 5 must lie above the straight line with a slope of 1.0. The expected relationship between the variables in Figure 5 depends upon both the underlying searching process and the spatial distribution of potential sets. While a positive relationship would be expected if both of these are random, a more precise definition is beyond the scope of this paper. The purpose in presenting Figures 5 and 6 is to display the range of differences in the success of vessels in locating potential fishing targets. The large variation among cruises suggests that all vessels may not be using the same searching strategy and is an important factor to keep in mind when considering the results from the clustering algorithm.

Description of Clusters

The clustering algorithm grouped between 30 and 100% of all sets and chases within a cruise into clusters with at least three members (Table 1). The percentage of all sets and chases that are included in clusters increases with the value of the cluster parameter so that 60–100% of all sets and chases within a cruise occur within 150 miles of another one. These percentages can only increase with increases in the value of the cluster parameter (i.e., a set that is included within a cluster for a lower value of the cluster parameter will always be included in a cluster at a higher value). Similarly, the average cluster size and the total percentage of the distance searched that occurs within clusters must be nondecreasing functions of the clustering parameter (Table 1). However, even when the clustering parameter equals 150 miles so that most sets occur within clusters, the percentage of the total distance searched within clusters averages only 59% of the total distance searched during the cruise. This indicates that substantial searching activity occurs far from any set or chase.

The average intercluster distance for a cruise ranged from 134 to 425 miles for clusters defined

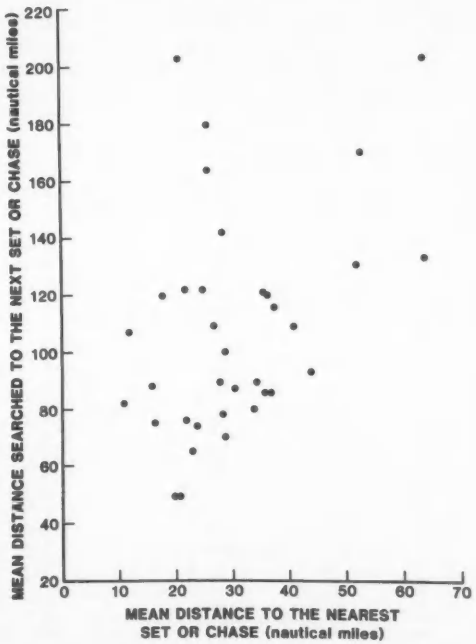

FIGURE 5.—The relationship between the average distance searched between sets and chases within a cruise and the average distance to the nearest one.

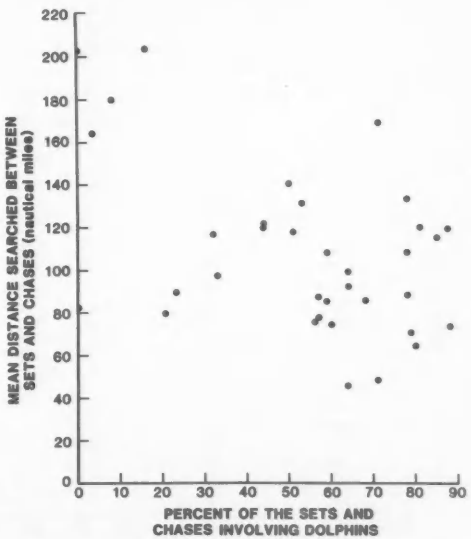

FIGURE 6.—The relationship between the average distance searched between sets and chases and the proportion of sets and chases in which schools of dolphins were associated for a cruise.

TABLE 1.—Statistics summarizing the results of the clustering algorithm showing the sensitivity to a range of values for the clustering parameter. Standard deviations are given as opposed to standard errors to provide an indication of the variation between cruises. All means are the simple average for 35 cruises.

		Cluster parameter			
		50	75	100	150
Percent of sets within clusters with at least 3 members	Mean	64	75	81	88
	SD	14.1	13.5	13.3	9.2
	Range	30–90	31–97	31–97	60–100
Average cluster radius for clusters with at least 3 members (nautical miles)	Mean	35	55	77	116
	SD	8.5	19.7	40.4	66.0
	Range	19–56	27–142	34–225	38–390
Percent of the searching within clusters with at least 3 members	Mean	25.8	39	47	59
	SD	12.6	16.4	16.1	10.6
	Range	9–61	16–91	19–91	31–91
Average intercluster distance (nautical miles)	Mean	210	261	297	356
	SD	65.9	75.9	82.2	100.9
	Range	134–425	155–465	173–513	196–691

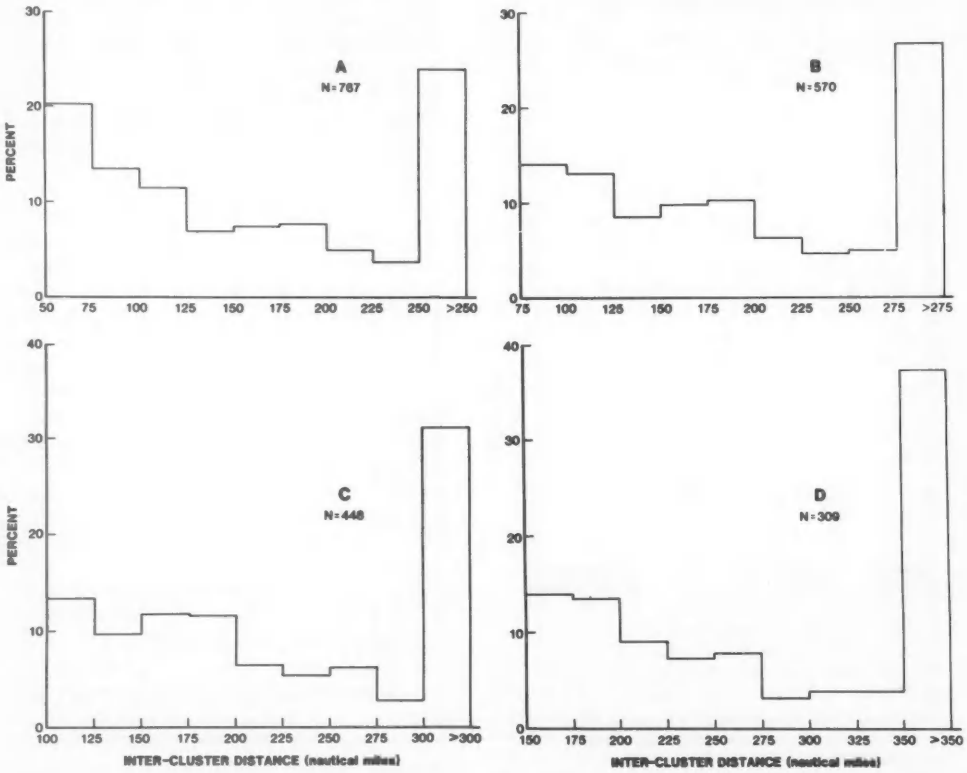

FIGURE 7.—The frequency distribution of intercluster distances. Distances from all cruises have been pooled. The values of the clustering parameter are A) 50, B) 75, C) 100, and D) 150.

by a value of 50 for the clustering parameter and from 196 to 691 miles for a value of 150 miles (Table 1). The frequency distribution of these intercluster distances (Fig. 7) is an indication of the stability of the clusters to the value of the clustering parameter. Thus, for a value of 100, over 65% of the clusters have an intercluster distance exceeding 175 miles. This suggests that 65% of clusters will be stable up to a value of 175 miles for the clustering parameter. (Note, this is not strictly true. If the set preceding the first member of a cluster was less than 175 miles away and this set was also less than 175 miles from the first set of the next cluster, this set plus these two clusters would be combined in a single cluster for a value of the cluster parameter less than 175.)

These statistics describing the characteristics of the defined clusters suggest that the algorithm used to create them successfully separates the activities of a cruise into areas where sets are common and areas where they are infrequent. The major differences in the clusters with different values for the clustering parameters result from the merging of two relatively close clusters or the inclusion of an isolated set or chase near the boundary of a cluster (e.g., for 80% of the cruises, the actual number of clusters decreases or remains the same over a range of 50–150 miles for the clustering parameter). However, the fact that many of these descriptive statistics vary continuously with the value of the clustering parameter suggests that these defined clusters do not represent distinct units, but areas of high concentration in a continuously grading system.

Cruises vary greatly with respect to the amount of variability they exhibit in response to changes in the value of the clustering parameter (Table 2). Such variability is to be expected since no single searching strategy is used by all vessels and vessels may change their strategy during the course of a cruise. In addition, the spatial distribution of potential sets probably also varies with time and space. These sources of variability among cruises, combined with the relatively small sample sizes within a cruise, may be part of the reason that the descriptive statistics characterizing clusters vary continuously with the value of the clustering parameter.

The lack of any sharp demarcation in the clusters as a function of the clustering parameter, combined with the large amount of variability exhibited among different cruises, creates a problem in presenting results based on the clustering algorithm. Consequently, whenever summary statistics are presented, results are given for a range of values for the clustering parameter.

TABLE 2.—Examples of the effect of changes in the value of the clustering parameter for 5 arbitrarily selected cruises.

Cruise	Value of the cluster parameter	Number of clusters with at least 3 members	Percent of sets and chases with clusters with at least 3 members	Average cluster radius for clusters with at least 3 members (nautical miles)	Percent of the searching within clusters with at least 3 members	Average intercluster distance (nautical miles)
1	50	4	90	32	61	171
	75	1	96	142	91	298
	100	1	96	142	91	298
	150	1	96	142	91	298
2	50	10	85	27	34	210
	75	7	97	61	60	294
	100	4	97	105	68	397
	150	4	98	126	71	443
3	50	5	30	27	9	402
	75	5	31	36	16	450
	100	5	31	46	19	479
	150	5	60	68	36	614
4	50	4	78	30	36	425
	75	4	80	39	41	465
	100	4	82	38	45	513
	150	4	82	38	45	513
5	50	1	65	45	38	302
	75	3	79	45	43	362
	100	3	79	45	43	362
	150	3	79	45	43	362

Whenever it seemed important to display the results by cruise, a value of 100 miles for the clustering parameter was used. It should be emphasized that the general patterns appear to be independent of the exact value of the clustering parameter.

Is Searching Different in Clusters?

To determine whether vessels tended to increase their searching effort in the vicinity of sets, the ratio of the total distance travelled (i.e., the distance searched plus the distance run) to the actual physical distances between sets was compared between and within clusters. This ratio is about 1.7 times greater in clusters than between clusters (Table 3). Also for no more than 7 cruises is the ratio within clusters less than the ratio between clusters (Table 3). By a sign test (Snedecor and Cochran 1967), these results imply that this ratio is significantly greater than 1.00 ($P < 0.005$).

In addition, the proportion of the total distance travelled that is devoted to searching is much greater when a vessel is between than when it is within clusters (Table 4). The fact that vessels run, and are not actively looking for tuna, proportionately more between than within clusters is an indication that clusters are areas in which a vessel has decided to remain. Vessels tend only to run at night. Usually, as long as the vessel is moving during daylight, the crew will be searching. Thus, large amounts of running tend to occur when vessels are actively moving to new areas.

TABLE 3.—Comparison between and within clusters of the ratio of the total distance travelled (i.e., distance searched plus distance run) to the actual physical distance between sets and chases. Means are the average values of the ratio for the 35 cruises being considered.

		Value of the cluster parameter			
		50	75	100	150
Between	Mean	1.79	1.70	1.65	1.59
	SD	0.064	0.062	0.060	0.065
	Range	1.24–2.70	1.13–2.71	1.12–2.68	1.11–2.81
Within	Mean	3.08	2.84	2.79	2.68
	SD	0.343	0.254	0.250	0.239
	Range	1.13–11.03	1.16–8.67	1.09–8.67	1.12–8.67
Number of cruises out of 35 in which the ratio is greater within than between clusters		[1]28	[1]31	[1]32	[1]31

[1] $P < 0.05$ of observing this many ratio greater within clusters than between if they were in fact equal based on a sign test (Snedecor and Cochran 1967).

TABLE 4.—Comparison between and within clusters of the ratio of the distance run without searching to the distance searched. Means are the average values of this proportion for the 35 cruises being considered.

		Value of the cluster parameter			
		50	75	100	150
Between clusters	Mean ratio	0.85	0.93	0.97	1.06
	SE	0.063	0.068	0.067	0.095
	Range	0.35–1.94	0.26–1.94	0.26–2.05	0.26–3.45
Within clusters	Mean ratio	0.29	0.33	0.38	0.46
	SE	0.040	0.036	0.042	0.048
	Range	0.01–0.88	0.04–0.98	0.04–1.13	0.05–1.06
Number of cruises out of a total of 35 in which the proportion is greater between clusters than within them		[1]34	[1]34	[1]34	[1]34

[1] $P < 0.001$ of observing the portion being greater between clusters than within 34 out of 35 cruises, if in fact the proportion was equal based on a sign test (Snedecor and Cochran 1967).

However, some running can still be expected within clusters because vessels mark favorable logs with radio transmitter in order to return to them at a latter time. It should be noted that three or more sets or chases rarely occur on the same day (Fig. 8). Therefore, the proportionately smaller amount of running that occurs within clusters is not an artifact resulting from clusters that do not span more than a single day.

Are Clusters Areas of High Spotted Dolphin Densities?

Encounter rates (total number of sightings of spotted dolphins divided by the total distance searched) tend to be much greater within clusters dominated by sets in association with dolphins than either within clusters dominated by non-dolphin sets or while searching between clusters (Table 5). The clustering algorithm would tend to ensure that such differences are likely to occur, but the magnitude of the differences is large and

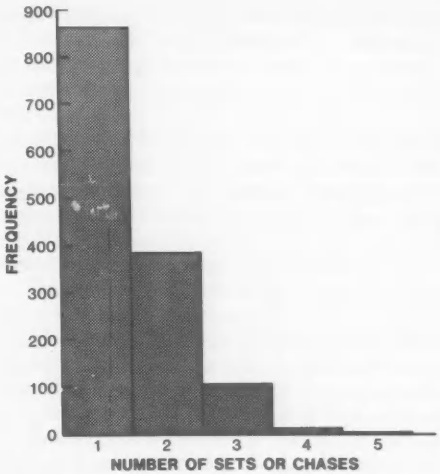

FIGURE 8.—The frequency distribution of the number of sets or chases during a day for all days on which there was at least one chase or set.

TABLE 5.—Comparison of encounter rates (number of schools of spotted dolphins, *Stenella attenuata*, per 100 miles searched) while searching within clusters classified according to the percentage of sets involving dolphins, and while searching between clusters. Unweighted means are the average value of the encounter within each cruise. Weighted means are based on the encounter rate weighted by the distance searched by a cruise and are equivalent to the total number of sightings divided by the total distance searched pooled across all vessels.

Value of the cluster parameter		Within clusters in which the percent of sets on dolphins ranged from 0–25	25–75	75–100	Between clusters
50	Unweighted mean	0.17	1.45	2.74	0.52
	SE	0.070	0.182	0.219	0.046
	Weighted mean	0.10	1.04	2.46	0.50
	SE	0.047	0.120	0.205	0.046
	Number of cruises	27	22	30	35
	Total distance searched (thousands of miles)	17.9	10.0	23.1	148.2
75	Unweighted mean	0.15	1.32	2.32	0.47
	SE	0.051	0.191	0.188	0.044
	Weighted mean	0.12	0.88	2.16	0.46
	SE	0.039	0.111	0.166	0.044
	Number of cruises	25	22	31	35
	Total distance searched (thousands of miles)	28.2	15.1	33.0	125.4
100	Unweighted mean	0.14	1.15	2.08	0.46
	SE	0.046	0.181	0.174	0.045
	Weighted mean	0.15	0.81	1.82	0.45
	SE	0.043	0.117	0.148	0.044
	Number of cruises	25	20	31	35
	Total distance searched (thousands of miles)	35.1	16.0	45.0	106.7
150	Unweighted mean	0.10	0.73	1.83	0.43
	SE	0.040	0.106	0.159	0.049
	Weighted mean	0.11	0.68	1.63	0.40
	SE	0.037	0.096	0.114	0.041
	Number of cruises	24	18	32	35
	Total distance searched (thousands of miles)	33.9	27.2	57.1	85.7

relatively insensitive to the value of the clustering parameter. However, the fact that a large percentage of the clusters tend to be dominated by either dolphin or non-dolphin sets is not a necessary consequence of the clustering algorithm and suggests that the two types of methods for locating and catching tuna tend to be spatially and temporally distinct. Encounter rates are substantially lower in clusters dominated by non-dolphin sets than when a vessel is searching between clusters (Table 5). This result is also not a necessary consequence of the clustering procedure and suggests that these clusters not only define areas of high densities of spotted dolphin schools but also areas of low densities.

Encounter rates could be lower in non-dolphin areas because of differences in detectability not related to the density of schools. For example, Hammond[4] suggested that the crew may scan closer to the vessel when searching in non-dolphin areas (see also Polacheck 1983). It seems unlikely that such factors could account for all of the differences between the encounter rates in Table 5.

Differences in detectability due to differences in weather conditions between and within clusters could also affect the results in Table 5. Encounter rates do decrease at higher Beaufort sea states (Polacheck 1983). However, little searching occurs above Beaufort state 4. The difference in encounter rates at Beaufort 0–2 compared with Beaufort 3–4 (about a factor of 1.28) is insufficient to explain the difference in Table 5 (Polacheck 1983). Moreover, areas of non-dolphin sets tend to be in nearshore areas with calmer seas and fishermen do not consider Beaufort 4 conditions as being too rough to fish.

Do Tuna Catches Differ Between and Within Clusters?

The average tons of tuna caught per set tend to be greater for sets which occur within clusters than sets between clusters (Fig. 9). For all values of the clustering parameter, the average catch per set was greater within than outside of clusters in approximately 70% of the cruises (Table 6). Parametric statistical comparisons of the average tons per set are not appropriate because of the large differences in the average catch per set among vessels (Fig. 9). A nonparametric sign test (Snedcor and Cochran 1966) suggests that the differences in catch per set between and within clusters are significant at least at the 0.05 probability level for all values of the clustering parameters that were considered.

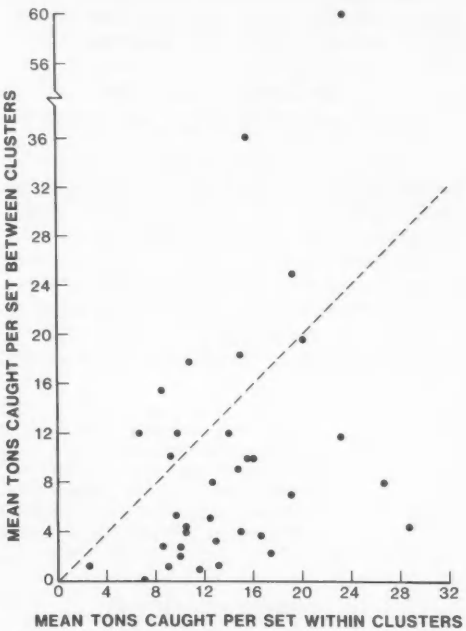

FIGURE 9.—The average tons of tuna caught per set while a vessel was travelling between clusters versus the average tons per set within clusters with at least three members. The dashed line represents the expected value if the catch rates were equal. The value of the cluster parameter equals 100.

TABLE 6.—The ratio of the tons of tuna caught per set within clusters with at least 3 members compared to tons caught per set between clusters. The means are the average values for the ratio within a cruise. Cruises in which 100% of the sets were within clusters are not inlcuded in the results.

	Value of the cluster parameter			
	50	75	100	150
Mean	1.73	2.02	2.98	2.76
SE	0.22	0.379	0.476	0.499
Range	0.41–6.83	0.23–11.18	0.39–11.68	0.43–8.43
n	35	34	34	25
Number of cruises in which ratio was greater than 1	[1]25	[1]25	[1]25	[1]19

[1]$P < 0.05$ of getting the observed number if the ratio equaled 1 by a sign test (Snedecor and Cochran 1966).

[4]Hammond, P. S. 1981. Some problems in estimating the density of dolphin populations in the eastern tropical Pacific using data collected aboard tuna purse seiners. Inter-Am. Trop. Tuna Comm. Intern. Rep.

Does Searching Behavior Bias the Overall Estimate of Dolphin Encounter Rates?

When the two different methods of estimating the overall encounter rates within a cruise are compared, the adjusted encounter rates tend to be smaller (Table 7). However, the differences are not large, not because the biases are necessarily small, but because positive and negative effect of concentrating searching effort tend to cancel each other. Positive biases would be expected in the unadjusted rate due to concentrating of searching effort in clusters dominated by sets made in association with dolphins, since these appear to be areas of high dolphin densities (Table 5). Similarly, negative biases would be expected due to searching in non-dolphin clusters. For the data considered here, substantial and roughly equal amounts of searching occurred in both types of clusters. The effects of concentrating searching effort within the two types of clusters tended to cancel each other. This suggests that the major effect of nonrandom searching on measures of relative abundance of dolphins will change in relationship to the importance of dolphin and non-dolphin fishing. Such changes tend to occur with changes in the relative abundance of large yellowfin tuna compared to skipjack and small yellowfin tuna.

DISCUSSION

The fundamental question in interpreting the results of this paper is whether the clusters that have been defined bear any relationship either to the searching strategy of the vessels or to the underlying distribution of dolphin and tuna schools. Two factors hamper answering this question: The first is the large variability among vessels; the second is the lack of appropriate null hypotheses by which to test the results. The large variability is to be expected and is inescapable. Not only is there a large stochastic element in the catch and encounter process, but large differences can be expected in searching strategies among vessels. Thus, a large range exist in skill and experience among fisherman. In addition, the amount of information, which is shared among vessels varies and some vessels may be acting as scouts for other vessels (Orbach 1975).

The specification of null hypotheses is difficult because an infinite number of searching models are compatible with the definition of random search (i.e., defining a random search as one in which the search path is independent of the distribution of the objects being sought). In order to actually model a random searching process, the probability of changing the direction of the search path needs to be specified. A random search could encompass anything from Brownian motion to random straight line crossings of an area. With a finite amount of searching, these will not necessarily yield the same results.

Most of the results from this paper are compatible with a model of clustered searching for clustered prey, and some of them seem hard to explain unless the searching and the schools of dolphins are nonrandomly distributed. That the distance travelled relative to the actual distances between sets tends to be greater in areas where the density of sets is high, as is the proportion of this distance which is spent searching, are unlikely results unless searching is concentrated in these areas. Also, the higher encounter rates in clusters dominated by dolphins, the comparisons of the distances and frequency of the nearest set with the preceding or next set, and the high percentage of sets which fall into clusters are results that would be expected if searching, tuna, and dolphins were

TABLE 7.—Comparison between the unadjusted overall encounter rate (number of schools of *Stenella attenuata* per 100 miles of searching) for a cruise and the encounter rate adjusted for possible bias due to the concentration of searching within clusters.

	Cluster parameter	Mean	SE	Range	Number of cruises out of 34 in which the corrected estimate was less than the uncorrected one[1]
Unadjusted		0.80	0.078	0.00–1.77	
Adjusted	50	0.73	0.074	0.00–1.66	27
	75	0.74	0.074	0.00–1.60	24
	100	0.75	0.077	0.00–1.73	21
	150	0.76	0.078	0.00–1.78	21

[1]One cruise had no recorded sighting of spotted dolphin schools.

spatially clustered. Perhaps the most surprising result in this context is that the average catch per set tends to be greater within the defined clusters than outside of them. There is nothing in the clustering algorithm that would tend to produce this result. If these larger catches per set reflect large schools of tuna, this argues that these defined clusters are areas where tuna tend to concentrate and not just areas of high densities of sets that could be found in any random distribution.

Within many of the cruises, the locations of two or more of the defined clusters overlap spatially (Fig. 10), indicating that vessels often return to an area after a period of searching elsewhere. In addition, clusters from different cruises overlap spatially and temporally. This overlapping of clusters indicates that the overall searching behavior is even more nonrandom than the results from this paper suggest. The overlapping both within and among cruises is a dimension that should be considered in future extensions to the present work.

Orbach (1975), in a nonquantitative, anthropological study of the purse seine fishery, included a general qualitative description of the searching behavior of the fishermen which supports many of

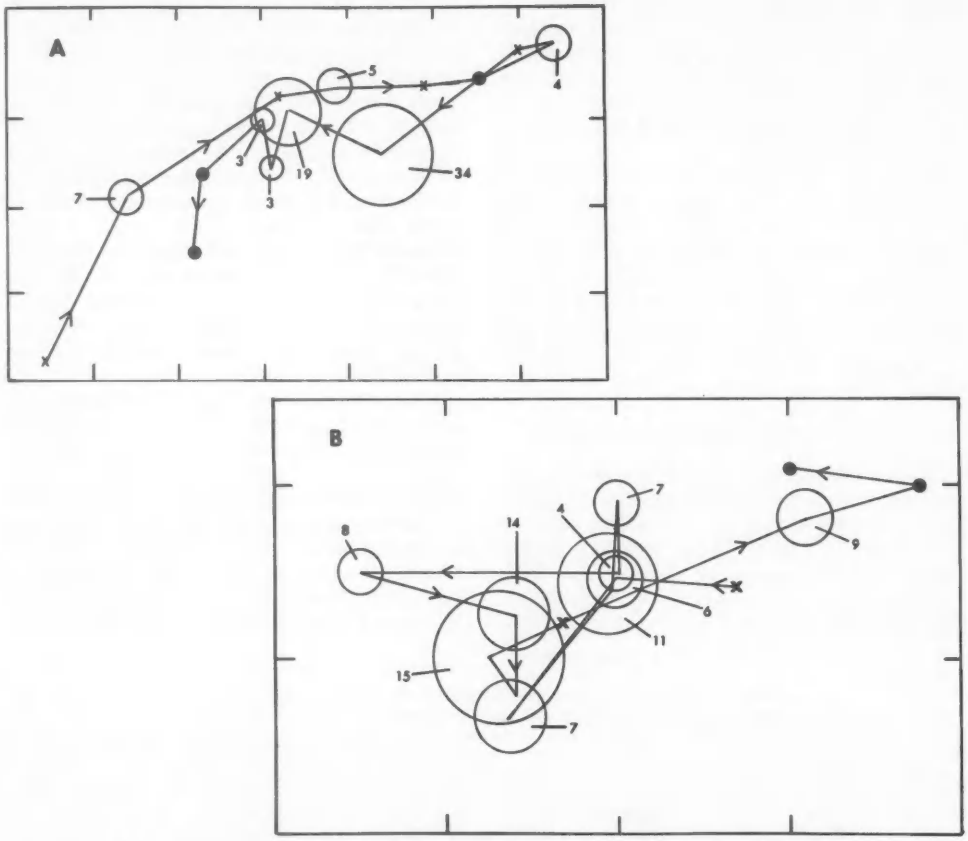

FIGURE 10.—Examples of the spatial relation between clusters for the two cruises depicted in Figure 2. Open circles indicate the position of all clusters with at least three members. The radius of each circle is scaled to the estimated radius of a cluster. The associated numbers are the number of sets and chases within a cluster. Solid circles indicate the position of clusters with only two members. Isolated sets are indicated by an ×. The value of the clustering parameter equals 100. Arrows indicate the order of movement between clusters. Note A and B are drawn to different scales. Distance between tick marks equals 300 miles. No geographic coordinates are given and the orientations were rotated at random so as not to compromise any proprietary fishing information.

the quantitative results in this paper. He stated that fishermen perceive two kinds of areas: The first, in which fishermen refer to their activity as "scratching", are regions where isolated schools of fish are encountered; the second, which fishermen refer to as an "area", are portions of the ocean where schools of tuna are congregated. He also reported that isolated tuna schools tend to be small. Fishermen prefer to concentrate in an "area" and actively search for them. I did not become aware of this study by Orbach until the final calculations of this paper were completed. Thus, his description is an independent indication that the results are not an artifact of the clustering algorithm.

The method used for estimating the location and size of a cluster could be refined. Such refinements were beyond the scope of the present work and would not affect any of the main results. However, such refinements might be important if the method used for calculating the adjusted encounter rates (Table 7) was used to develop relative abundance indices for dolphins in the ETP. As pointed out by one reviewer, the problem of estimating the shape, size, and location of a cluster is analogous to the problem of determining the home range for an animal from a set of observed positions over time (Sanderson 1966; Cooper 1978; Schoener 1981; Swihart and Slade 1985) and is part of the more general problem of how to estimate the limits and size of clusters from any clustering algorithm. The methods used for estimating home ranges cannot be directly applied to the tuna boat observer data but might provide a basis for developing a better estimator for these statistics relating to cluster size in any extension to the present work.

To the extent that the results from this paper indicate that searching is clustered, they suggest that when these data are used for estimating relative densities of dolphin schools, or when catch and effort data from purse seiners are used to assess tuna stocks, rather fine geographic stratifications are needed to avoid biases from the nonrandom searching within a cruise. The estimates of the cluster radius could be considered as a guide to appropriate levels of stratification. For example, from 31 to 46% of all clusters with at least three members had a radius of less than 60 miles (Fig. 11). This suggests that at a minimum,

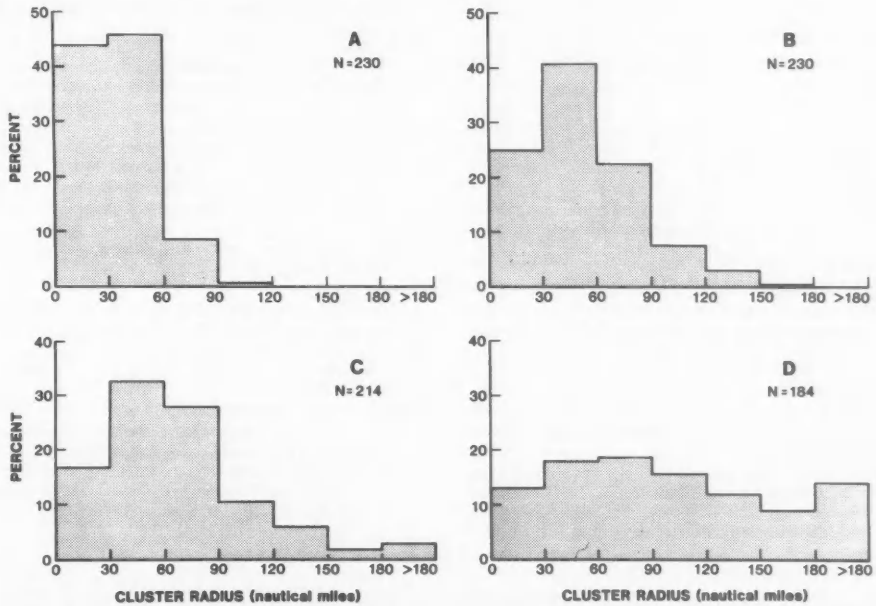

FIGURE 11.—The frequency distribution for estimated radii for all clusters with at least three members. Estimates from all cruises have been pooled. The values of the clustering parameter are A) 50, B) 75, C) 100, and D) 150.

a 2° stratification would be necessary to avoid biases in these areas.

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LITERATURE CITED

ALLEN, R., AND R. PUNSLEY.
1984. Catch rates as indices of abundance of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm. 18:303–379.

BLACKBURN, M., AND F. WILLIAMS.
1975. Distribution and ecology of skipjack tuna, *Katsuwonus pelamis*, in an offshore area of the eastern tropical Pacific. Fish. Bull., U.S. 73:382–411.

CALKINS, T. P.
1963. An examination of fluctuations in the "concentration index" of purse seiners and bait boats in the fishery for tropical tuna in the eastern Pacific. Inter-Am. Trop. Tuna Comm. Bull. 8:255–316.

CALKINS, T. P., AND B. M. CHADWIN.
1967. Geographical distribution of yellowfin tuna and skipjack catches in the eastern Pacific Ocean, by quarters of the year 1963–1966. Inter-Am. Trop. Tuna Comm. Bull. 12:435–508.
1971. Geographical catch of yellowfin and skipjack tuna in the eastern tropical Pacific Ocean, 1967–1970, and fleet and total catch statistics. Inter-Am. Trop. Tuna Comm. Bull. 15:285–377.

CLARK, C. W., AND M. MANGEL.
1983. Search theory in ecology and resouce management. *In* M. Freedman (editor), Proceedings of the International Conference on Population Biology, p. 380–388. Springer Lecture Notes in Biomathematics, Vol. 52. Springer Verlag, N.Y.

COOPER, E.
1979. Home range criteria based on temporal stability of areal occupation. J. Theor. Biol. 73:687–695.

GULLAND, J. A.
1955. Estimation of growth and mortality in commerical fish populations. Fish. Invest. Minist. Agric. Fish. Food (G.B.), Series 2, 18:1–46.

HELLAND-HANSEN, B.
1909. Statistical research into the biology of the haddock and cod in the North Sea. Rapp. P-v Réun 10:1–62.

KOOPMAN, B. O.
1980. Search and screening. Pargamon Press, N.Y., 509 p.

ORBACH, M. K.
1975. The cultural system of the tuna seinermen of San Diego, California. Ph.D Thesis, Univ. California, San Diego, CA, 411 p.

PAZYNICH, G. I.
1966. Primery primeneniya teorii statisticheskiskh reshenii k zadacham taktiki promysla (Examples of the application of statistical-solution theory to problems in the fishing tactics). Noe Khoz. 6:80–81. (Translation available in the library of National Marine Fisheries Service Northeast Fishery Laboratory, Woods Hole, MA.)

PERRIN, W. F.
1968. The porpoise and the tuna. Sea Frontiers 14:166–174.
1969. Using porpoise to catch tuna. World Fishing 18:42–45.

POLACHECK, T.
1983. The relative abundance of dolphins in the eastern tropical Pacific based on encounter rates with tuna purse seiners. Ph.D Thesis, Univ. Oregon, Eugene, OR, 444 p.

SALIA, S. B., AND J. M. FLOWERS.
1979. Elementary applications of search theory to fishing tactics as related to some aspects of fish behavior. F.A.O. Conference on Fish Behavior in Relation to Fishing Techniques and Tactics, p. 343–355.

SANDERSON, G.
1966. The study of mammal movements - a review. J. Wildl. Manage. 30:215–235.

SCHOENER, T. W.
1981. An empirically based estimate of home range. Theor. Popul. Biol. 20:281–325.

SNEDECOR, G. W., AND W. C. COCHRAN.
1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, 593 p.

SUZUKI, Z., P. K. TOMLINSON, AND M. HONMA.
1978. Population structure of Pacific yellowfin tuna. Inter-Am. Trop. Tuna Comm. Bull. 17:277–411.

SWIHART, R. K., AND N. A. SLADE.
1985. Influence of sampling interval on estimates of home range size. J. Wildl. Manage. 49:1019–1025.

A COMPREHENSIVE THEORY ON THE ETIOLOGY OF BURNT TUNA

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ABSTRACT

Over the past 14 years, the Hawaii handline fishery has experienced phenomenal growth in the catch for large yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *Thunnus obesus*. These fish are primarily caught for the sashimi (raw consumption) market but have been continually plagued with a product quality problem known as "burnt tuna" or, in Japanese, yake niku. Not only does this problem significantly reduce the value of the catch, it also limits export markets and expansion of this low-capital, high-return fishery to other areas of the Pacific. Previous research and suggestions for mitigating burnt tuna have centered on the hypothesis that it is caused by high muscle temperature and low pH, which is the result of a violent struggle during capture.

A new, more comprehensive hypothesis is presented: Burnt tuna is actually caused by the postmortem activation of enzymes known as calcium-activated proteases and by the enhancement of the effect of these enzymes by high blood catecholamine levels. Previously unexplainable observations, such as the propensity of female fish to become burnt more often during the summer months, the efficacy of brain destruction in preventing burnt tuna, and the lack of effect of cooling on the incidence of burnt tuna, are explainable in light of this new hypothesis.

One of the largest fisheries in Hawaii is the handline fishery for large (>50 kg) yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *T. obesus*, caught primarily for raw consumption as sashimi. Yearly landings increased from 89 short tons (ex-vessel value, $131,000) in 1973 to 615 short tons (ex-vessel value, $2.1 million) in 1984 (Yuen 1979; Hudgins and Pooley 1987). The total economic value of the fishery has been estimated as high as $5 million yearly (Ikehara[4]). In Hawaii, the night handline fishery is known as ika shibi from the Japanese words for squid and tuna, and the daytime fishery is known as palu ahi from the Hawaiian words for chum and yellowfin tuna. There is also growing international interest in this type of fishing because of its low initial capital investment, low operating and fixed expenses, strong export markets, and high profitability (Strong 1979; Gibson 1981; Jerrett 1984). Boats can be as small as 6 m and require only one- or two-man crew. Catch rates in Hawaii have ranged from two fish per hook per night (Yuen 1979) to one-half fish per hook per night (Bourke[5]), illustrating the profitability for the individual fisherman.

Unfortunately, handline (as well as primarily recreational trolling) fishermen are plagued by a product quality problem known as "burnt tuna" or, in Japanese, as yake niku (literally translated as "cooked meat"). When fish are intended for raw consumption, product quality is of utmost importance. Prime quality tuna flesh should be red, translucent, and firm and have a delicate flavor. Burnt tuna is pale, exudes a clear fluid, and has a soft texture and a slightly sour taste. Although perfectly palatable when cooked or canned, burnt tuna is considered unsuitable for raw consumption and commands only a fraction of the price of prime quality fish. Fish are usually exported whole to preserve freshness, so burnt tuna often is not detected until shipping costs have been incurred. This discourages exports of tuna caught from areas or via fishing techniques with high incidences of the problem.

Burnt tuna affects from 5 to 100% of the tissue from an individual fish and ranges from mild to severe. Approximately 25% of the fish caught by the Hawaii handline fishery are burnt, as are 50% of the large yellowfin tuna caught by commercial and recreational trollers (Bourke fn. 5).

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[4]Ikehara, W. N. 1981. A survey of the ika-shibi fishery in the State of Hawaii, 1980. Southwest Fish. Cent. Adm. Rep. H-82-4C, 12 p. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396.

[5]Bourke, R. E. 1985. Hilo ikashibi fishery 1984 survey: Problems of a maturing fishery and a potential solution to the burnt tuna problem. Poster presentation at 1985 Tuna Conference.

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FISHERY BULLETIN: VOL. 86, NO. 2, 1988.

Annual losses to the handline fishery are an estimated 16% of the value of the total catch (Cramer et al. 1981). The problem has also been reported in fish intended for raw consumption caught by purse seine (Nakamura et al. 1977). Surprisingly, the problem rarely occurs in fish caught by longlining (Williams 1986).

PAST RESEARCH ON BURNT TUNA

The Japanese were the first to investigate the causes of burnt tuna and possible mitigating strategies (Itokawa 1968, 1969). The first controlled laboratory investigations were those of Nakamura et al. (1977) and Konagaya and Konagaya (1978, 1979). Nakamura et al. (1977) concluded that high muscle temperature and low muscle pH caused myofibrillar protein denaturation and also noticed that, once denaturation began, it continued even if the tissue was kept at 0°C. Because of the relatively high thermostability of tuna myofibrillar protein and because yake niku occurs in species (e.g., frigate mackerel and sardine) that do not generate high muscle temperatures during struggling, Konagaya and Konagaya (1978) concluded that acid denaturation of myofibrillar proteins at moderate temperatures was the underlying cause.

Cramer et al. (1981) studied handline-caught yellowfin tuna in Hawaii and found that the occurrence of burnt tuna did not correlate with muscle temperature at time of landing and correlated only loosely with extracellular muscle pH. Ikehara[6] conducted an engineering study to develop methods to cool large yellowfin tuna more rapidly, the presumption being that rapid cooling would prevent muscle degradation. Although successful in developing a technique to increase cooling of deep muscle temperature, as shown in Figure 1, there was no apparent correlation between rate of cooling and incidence of burnt flesh. In spite of this lack of directly observed correlation, some publications designed for fishermen still stress that high muscle temperatures and low muscle pH are the prime causes of burnt tuna (Gibson 1981). Others have expressed doubt as to the validity of this hypothesis (Jerrett 1984).

The high muscle temperature-low pH hypothesis appears to fit with what is known about tuna physiology, in that these fishes are capable of producing muscle temperatures significantly above ambient (Carey et al. 1971; Carey 1973) and exhibit some of the highest rates of muscle glycolysis (production of muscle lactate and concomitant production of acidity) observed in nature (Hochachka et al. 1978; Hochachka and Mommsen 1983). Yet some observations do not fit this hypothesis. For example, burnt tuna occurs more frequently in summer, more frequently in female fish, and more frequently in fish fought for short periods of time than in fish fought for long periods (>7 minutes or <2 hours) (Davie and Sparksman 1986; Nakamura[7]). Furthermore, burnt tuna occurs rarely in longline-caught fish and in fish subjected to brain or spinal column destruction immediately following capture (Nakamura et al. 1977; [Suisan Sekai] 1977; Cramer et al. 1981; Davie and Sparksman 1986; Nakamura fn. 7). The hypothesis that burnt tuna is caused by high muscle temperature and low muscle pH does not seem to directly fit with any of these observations.

A NEW ANALYSIS OF THE BURNT TUNA PROBLEM

At the biochemical level, the high muscle temperature-low pH hypothesis would predict that the observed drop in extracellular pH would be accompanied by a similar drop in intracellular pH and activation of lysosomal proteases. These proteases would then degrade actin and myosin, the dominant muscular proteins, resulting in the

[6]Ikehara, W. N. 1981. Development of a small-boat chilling system for the reduction of burnt tuna. Final Report for a Pacific Tuna Development Foundation contract, var. pag.

[7]R. Nakamura, Department of Animal Sciences, University of Hawaii, Honolulu, HI 96822, pers. commun. October 1987.

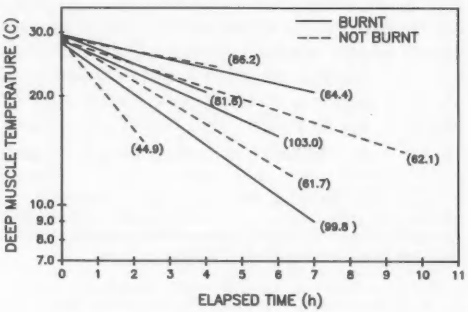

FIGURE 1.—Data are from Ikehara (text fn. 6). Initial and final deep muscle temperatures are plotted on semilogarithmic axes to linearize the rate of temperature change. Numbers in parentheses are the body weight (kg) for each fish.

undesirable changes seen in burnt tuna. The lysosomal proteases, specifically cathepsins B, D, and L, have an optimum pH of about 5 (Dahlmann et al. 1984). However, recent work by Abe et al. (1985, 1986) has shown that, intracellularly, tuna muscle is well buffered and that a fall in extracellular pH is not necessarily accompanied by an equivalent fall in intracellular pH. Using ischemic rat gastrocnemius muscle, Hagberg (1985) found that a 1 pH unit drop (7.30–6.36) in extracellular pH was accompanied by a drop in intracellular pH of only 0.4 unit (7.00–6.60). Thus, the acidic intracellular environment that would favor the action of the lysosomal proteases probably is not present in burnt tuna. Also, with the exception of calcium-activated neutral protease, all other muscle proteases (cathepsins B, D, L; alkaline serine protease; neutral trypsin-like protease; and alkaline cysteinyl protease) degrade myosin (Dahlmann et al. 1984). Yet Hochachka and Brill (1987) found burnt muscle had no increase in 3-methyl-histidine, a specific marker for myosin breakdown. Decomposition of other myofibrillar proteins is, therefore, implicated.

Electronmicrographs of postmortem burnt tuna muscle (Davie and Sparksman 1986) showed a consistent, rapid disintegration of Z-discs and irregularities in the sarcoplasmic reticulum (SR). The changes in burnt muscle were not different in kind from postmortem changes seen in unburnt tissue, but were a result of a significant increase in the rate of disintegration. Selected destruction of the Z-discs, troponin and tropomyosin, and the SR is characteristic of a pair of proteases known as calcium-activated neutral proteases (CANP's) (Sugita et al. 1984; Suzuki et al. 1984). These proteases are cytoplasmic, ubiquitous, activated by increased intracellular calcium levels, and active at pH 5.5–8.0 (Sakamoto and Seki 1985; Koohmaraie et al. 1986; Seki and Kimura 1986; Zeece et al. 1986b). The intracellular pH most likely found in burnt tuna muscle is, therefore, more consistent with CANP action than with lysosomal proteases whose activity requires a pH closer to 4.5 (Hochachka and Brill 1987). In addition, while cathepsin D's activity is greatly restricted at 15°C, CANP is still active at 5°C (Koohmaraie et al. 1986; Zeece et al. 1986a).

A new etiology of burnt tuna proposed by Hochachka and Brill (1987) is summarized in Figure 2. Their hypothesis predicts that low intracellular ATP concentrations lead to the leaking of Ca^{++} into the cell and increases in intracellular

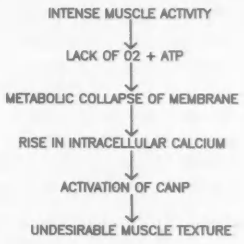

FIGURE 2.—Biochemical reactions involved in the development of burnt tuna as proposed by Hochachka and Brill (1987).

Ca^{++} concentrations. These increases, in turn, activate CANP, which specifically attacks troponin, tropomyosin, SR, and mitochondria. The breakdown of the latter two intracellular organelles releases more calcium into the cytoplasm, thus further increasing the activity of CANP.

The effect of brain and spinal cord destruction on reducing the incidence of burnt tuna and of similar muscle degradation seen in other fish species can be explained by this new hypothesis, which assumes the initial drop in ATP is the root cause of the elevated intracellular calcium (Amano et al. 1953; Fujimaki and Kojo 1953; Konagaya and Konagaya 1978; Ikehara fn. 6). Brain destruction maintains elevated muscle ATP levels after capture (Boyd et al. 1984). Data recently collected on the use of brain and spinal cord destruction in large yellowfin tuna (Fig. 3)

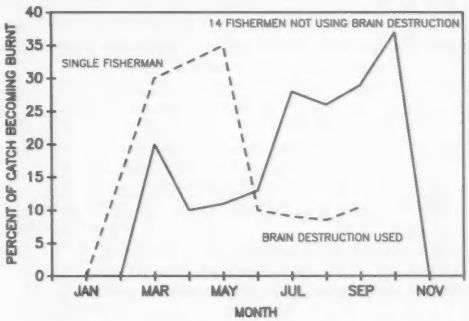

FIGURE 3.—Incidence of burnt tuna occurring in large yellowfin tuna caught by 14 commercial handline fishermen operating out of Hilo, HI, January–September 1984, and by 1 fisherman who began using brain destruction in May. His incidence of fish becoming burnt dropped dramatically in spite of the normal summer increased incidence seen in the catch of 14 other fishermen.

clearly show the effectiveness of this technique in preventing burnt tuna. A drop from 30 to <10% of the tuna becoming burnt was noted when the fisherman changed his killing technique from shooting to the use of a brain spike.

A MORE COMPREHENSIVE HYPOTHESIS ON THE ETIOLOGY OF BURNT TUNA

The hypothesis presented by Hochachka and Brill (1987) does not explain all the observed factors leading to tunas' different propensity to become burnt. It cannot explain why tunas struggling for <7 minutes rarely become burnt (Nakamura fn. 7), nor can it account for the observations of Davie and Sparksman (1986) and Bourke (unpubl. data), who found that tuna struggling for extended (>1 hour) periods of time have a lower probability of becoming burnt. It also cannot explain why female fish become burnt more often than males (Nakamura et al. 1977), or why fish caught in summer become burnt more often (Fig. 3).

Our revised hypothesis is presented in Figure 4. We have incorporated into the Hochachka and Brill (1987) hypothesis, the action of the neurotransmitters-hormones norepinephrine (NE) and epinephrine (E) (collectively referred to as catecholamines). Periods of intense physical activity or capture stress increase the levels of circulating catecholamines by about 10–200 times in fish other than tunas (Nakano and Tomlinson 1967; Ling and Wells 1985). Most likely a similar situation occurs in tuna during hooking, fighting, and capture. The importance of elevated circulating catecholamines in this particular schema comes from their potentiating effect on the action of CANP. Catecholamines cause the phosphorylation of troponin, resulting in a more rapid and prolonged proteolysis of this muscle structure (Toyo-oka 1982); in other words, high circulating levels of catecholamines greatly increase the effectiveness of the enzymes responsible for a tuna becoming burnt.[8]

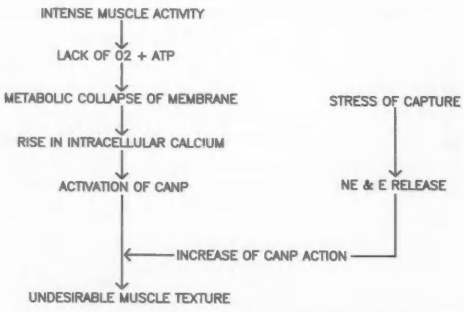

FIGURE 4.—Comprehensive theory of the etiology of burnt tuna proposed in this paper.

The gills are the organ primarily responsible for the degradation of catecholamines, and circulating catecholamines are rapidly cleared from the blood (Nekvasil and Olson 1986). We estimate circulating catecholamines in tuna have a half-life of 30 minutes or less. Therefore, we hypothesize that, in a longline-caught fish remaining in the water for several hours after hooking (Davie and Sparksman 1986), plasma catecholamines are reduced to low levels before the fish is landed and killed, thus resulting in a low percentage of burnt fish. Similarly, fish caught by rod and reel or by handline and fought for several hours would have the low circulating catecholamine levels and low propensity to become burnt. Indeed, Gibson (1981) recommends that handline-caught fish be attached to a buoy and left for an hour prior to being brought on board and killed, as a measure to prevent burnt tuna. That this technique presumably lowers blood catecholamine levels prior to death could explain its efficacy. On the other hand, we hypothesize that a fish landed during the peak of its blood catecholamine concentrations would have the greatest propensity for becoming burnt. This indeed appears to be the case.

The mechanism that ties catecholamines to the observed seasonality and increased number of female fish becoming burnt lies in the biochemical structural similarity of catecholamines and reproductive steroids, particularly estrogen. These steroids reach a peak during spawning season, which is May through October for yellowfin tuna in Hawaii (June 1960). A corresponding increase occurs in the percentage of the tuna catch that becomes burnt during this season (Fig. 3). In the presence of tyrosine hydroxylase, estrogen is converted to catecholestrogen and consequently competes for the same degradative enzymes in the gills, therefore slowing the clearance of catecholamines from the blood (Nekvasil and Olson 1986). Female fish, with high circulating estrogen levels, would then be expected either to reach

[8]Although cortisol is also known to be released during stress, its mechanism of action is much slower than NE or E, making it unlikely that it could exert catabolic effects within 15 minutes.

higher maximum circulating catecholamine levels or to maintain high levels for longer periods, thus explaining the greater number of female fish that become burnt and the seasonality of the occurrence of burnt tuna.

As pointed out by Davie and Sparksman (1986) and Hochachka and Brill (1987), burnt tuna is a quantitative change in tissue decomposition, not a qualitative one. High blood catecholamine levels at the time of death act as accelerators in this inevitable metabolic cascade. However, because we are dealing with a change in rate, the action of catalysts can make all the difference as to whether or not a fish becomes burnt due to CANP.

FUTURE RESEARCH

Under normal conditions, CANP is inhibited by calpastatins. This class of proteins is distinct from the other cysteine protease inhibitors, the cystatins. Although the cystatins can inhibit cathepsins B and H, they are unable to alter CANP activity. Conversely, calpastatin is only effective against calcium-activated neutral protease (Barrett et al. 1986; Parkes 1986). Unfortunately, almost nothing else is known about the relationship of CANP to its endogenous inhibitor, either structurally or physiologically. Certainly investigations into the role of calpastatin would prove valuable for this research.

Immediate future research will concentrate on tracking the specific action of CANP in burnt tuna and attempting to stop this action with Ca^{++} chelating agents such as EGTA (ethyleneglycolbis-(aminoethyl ether)-N,N,N′,N′-tetraacetic acid) or by use of its intracellular inhibitor, calpastatin. Also, blood catecholamine levels of stressed and unstressed fish will be measured, along with metabolic clearance rates of norepinephrine and epinephrine.

When viewed as a process of metabolic deregulation of CANP, the rapid deterioration of tuna muscle ceases to be an isolated muscular phenomenon. The Z-disc disintegration characteristic of burnt tuna is also present in cardiac muscle injury due to ischemia and muscular dystrophy (Sugita et al. 1984). Given the highly conserved nature of muscle tissue, an understanding of burnt tuna may also provide insights into the metabolic processes of human disease.

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LITERATURE CITED

ABE, H., R. W. BRILL, AND P. W. HOCHACHKA.
1986. Metabolism of L-histidine, carnosine, and anserine in skipjack tuna. Physiol. Zool. 59:439–450.

ABE, H., G. P. DOBSON, U. HOEGER, AND W. S. PARKHOUSE.
1985. Role of histidine-related compounds to intracellular buffering in fish skeletal muscle. Am. J. Physiol. 249:R449–R454.

AMANO, K., M. BITO, AND T. KAWABATA.
1953. Handling effect upon biochemical change in the fish muscle immediately after catch—I. Difference of glycolysis in the frigate mackerel killed by various methods. Bull. Jpn. Soc. Sci. Fish. 19:487–498.

BARRETT, A. J., N. D. RAWLINGS, M. E. DAVIES, W. MACHLEIDT, G. SALVESEN, AND V. TURK.
1986. Cysteine proteinase inhibitors of the cystatin superfamily. *In* A. Barrett and G. Salvesen (editors), Proteinase inhibitors, p. 515–569. Elsevier Sci. Publ. BV, North Holland.

BOYD, N. S., N. D. WILSON, A. R. JERRETT, AND B. I. HALL.
1984. Effects of brain destruction on post harvest muscle metabolism in the fish kahawai (*Arripis trutta*). J. Food Sci. 49:177–179.

CAREY, F. G.
1973. Fishes with warm bodies. Sci. Am. 228:36–44.

CAREY, F. G., J. M. TEAL, J. W. KANWISHER, AND K. D. LAWSON.
1971. Warm–bodied fish. Am. Zool. 11:137–145.

CRAMER, J. L., R. M. NAKAMURA, A. E. DIZON, AND W. N. IKEHARA.
1981. Burnt tuna: Conditions leading to rapid deterioration in the quality of raw tuna. Mar. Fish. Rev. 43(6):12–16.

DAHLMANN, B., L. KUEHN, AND H. REINAUER.
1984. Proteolytic enzymes and enhanced muscle protein breakdown. *In* W. H. Horl and A. Heidland (editors), Proteases, p. 505–517. Plenum Press, N.Y.

DAVIE, P. S., AND R. I. SPARKSMAN.
1986. Burnt tuna: An ultrastructural study of postmortem changes in muscle of yellowfin tuna (*Thunnus albacares*) caught by rod and reel and southern bluefin tuna (*Thunnus maccoyii*) caught on handline or longline. J. Food Sci. 51:1122–1128, 1168.

FUJIMAKI, M., AND K. KOJO.
1953. Handling effect upon biochemical change in the fish muscle immediately after catch—II. Changes of acid-soluble phosphorus compounds of frigate mackerel muscle. Bull. Jpn. Soc. Sci. Fish. 19:499–504.

GIBSON, D. J. M.
1981. A handbook on processing southern bluefin tuna for the fresh chilled sashimi market in Japan. Minist. Agric. Fish., Wellington, var. pag.

HAGBERG, H.
1985. Intracellular pH during ischemia in skeletal muscle: Relationship to membrane potential, extracellular pH, tissue lactic acid and ATP. Pfluegers Arch. 404:342–347.

HOCHACHKA, P. W., AND R. W. BRILL.
In press. Autocatalytic pathways to cell death: A new analysis of the tuna burn problem. Fish Physiol. Biochem. 3.

HOCHACHKA, P. W., W. C. HULBERT, AND M. GUPPY.
1978. The tuna power plant and furnace. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 153–174. Acad. Press, N.Y.

HOCHACHKA, P. W., AND T. P. MOMMSEN.
1983. Protons and anaerobiosis. Science (Wash. D.C.) 219:1391–1397.

HUDGINS, L. L., AND S. G. POOLEY.
1987. Growth and contraction of domestic fisheries: Hawaii's tuna industry in the 1980s. *In* D. J. Doulman (editor), Tuna issues and perspectives in the Pacific islands region, p. 225–241. East-West Center Press, Honolulu.

ITOKAWA, S.
1968. On maintaining the freshness of tuna seine catches. Reports of the Mie Prefecture Owase Fishery Experiment Station, p. 1–15.
1969. On experiments in prevention of burnt flesh in yellowfin tuna. Rep. Mie Pref. Owase Fish. Exp. Stn. p. 1–9.

JERRETT, A. R.
1984. Detection and prevention of burning in southern bluefin tuna. Part A: Research results and discussion. Fish Processing Bull. 4, 22 p. + app.

JUNE, F. C.
1960. Spawning of yellowfin tuna in Hawaiian waters. Fish. Bull., U.S. 54:47–64.

KONAGAYA, S., AND T. KONAGAYA.
1978. Denaturation at moderate temperatures of myofibrillar protein of red-meat fish: A possible cause of yake-niku. Bull. Tokai Fish. Res. Lab. 96:67–74.
1979. Acid denaturation of myofibrillar protein as the main cause of formation of "yake-niku", a spontaneously done meat, in red meat fish. Bull. Jpn. Soc. Sci. Fish. 45:245.

KOOHMARAIE, M., J. E. SCHOLLMEYER, AND T. R. DUTSON.
1986. Effect of low–calcium–requiring calcium activated factor on myofibrils under varying pH and temperature conditions. J. Food Sci. 51:28–32, 65.

LING, N., AND R. M. G. WELLS.
1985. Plasma catecholamines and erythrocyte swelling following capture stress in a marine teleost fish. Comp. Biochem. Physiol. 82C:231–234.

NAKAMURA, K., Y. FUJII, AND S. ISHIKAWA.
1977. Experiments on the prevention of "burning" of tunas—I. An examination of causes of occurrence. Bull. Tokai Reg. Fish. Res. Lab. 90:39–43. (Engl. transl. by W. G. Van Campen, 1980, 8 p., Transl. No. 46; available Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)

NAKANO, T., AND N. TOMLINSON.
1967. Catecholamine and carbohydrate concentrations in rainbow trout (*Salmo gairdneri*) in relation to physical disturbance. J. Fish. Res. Board Can. 24:1701–1715.

NEKVASIL, N. P., AND K. R. OLSON.
1986. Extraction and metabolism of circulating catecholamines by the trout gill. Am. J. Physiol. 250:R526–R531.

PARKES, C.
1986. Calpastatins. *In* G. Barrett and A. Salvesen (editors), Proteinase inhibitors, p. 571–587. Elsevier Sci. Publ. BV, North Holland.

SAKAMOTO, S., AND N. SEKI.
1985. Limited hydrolysis of carp myosin by calpains. Bull. Jpn. Soc. Sci. Fish. 51:1551–1557.

SEKI, N., AND Y. KIMURA.
1986. Degradation of troponin and tropomyosin by calpain. Bull. Jpn. Soc. Sci. Fish. 52:1673–1680.

STRONG, R. D.
1979. 1978–79 PTDF funded feasibility study to establish an ika-shibi fishery on Guam—Final Report. Pac. Tuna Dev. Found., May 1979, var. pag.

SUGITA, H., S. ISHIURA, K. KAMAKURA, H. NAKASE, K. HAGIWARA, I. NONAKA, AND K. TOMOMATSU.
1984. Ca-activated neutral protease in physiological and pathological conditions. *In* S. Ebashi, M. Endo, K. Imahori, S. Kakiuchi, and Y. Nishizuka (editors), Calcium regulation in biological systems, p. 243–256. Acad. Press, Tokyo.

[SUISAN SEKAI]
1977. How to effectively kill tunas in order to maintain quality and higher prices. Suisan Sekai 9:52–57. (Engl. transl. by T. Otsu, 1978, 4 p., Transl. No. 25; available Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396).

SUZUKI, K., S. KAWASHIMA, AND K. IMAHORI.
1984. Structure and function of Ca^{2+}-activated protease. *In* S. Ebashi, M. Endo, K. Imahori, S. Kakiuchi, and Y. Nishizuka (editors), Calcium regulation in biological systems, p. 213–226. Acad. Press, Tokyo.

TOYO-OKA, T.
1982. Phosphorylation with cyclic adenosine 3′:5′ monophosphate-dependent protein kinase renders bovine cardiac troponin sensitive to the degradation by calcium-activated neutral protease. Biochem. Biophys. Res. Commun. 107:44–50.

WILLIAMS, S. C.
1986. Marketing tuna in Japan. Queensl. Fish. Ind. Train. Comm., Brisbane, Queenl., Aust., 60 p.

YUEN, H. S. H.
1979. A night handline fishery for tunas in Hawaii. Mar. Fish. Rev. 41(8):7–14.

ZEECE, M. G., K. KATOH, R. M. ROBSON, AND F. C. PARRISH, JR.
1986a. Effect of cathepsin D on bovine myofibrils under different conditions of pH and temperature. J. Food Sci. 51:769–772, 780.

ZEECE, M. G., R. M. ROBSON, M. L. LUSBY, AND F. C. PARRISH, JR.
1986b. Effect of calcium activated protease (CAF) on bovine myofibrils under different conditions of pH and temperature. J. Food Sci. 51:797–803.

REPRODUCTIVE BIOLOGY OF THE SPOTTED SEATROUT, *CYNOSCION NEBULOSUS*, IN SOUTH TEXAS[1]

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ABSTRACT

The spotted seatrout, *Cynoscion nebulosus*, spawns from April through the end of September in shallow bays in South Texas. All females were sexually mature at 300 mm SL and males at 200 mm SL. Histological examination of the testes showed that spermatogenesis began in January and continued until September, although spermatozoa remained in the testes until November. Spermatogenesis was more active in the peripheral lobules of the testes than in the central lobules during the latter half of the spawning season. The sequence and timing of final oocyte maturation (FOM) was investigated for the first time in this species. Lipid coalescence began at dawn and germinal vesicle migration started by midmorning. By early afternoon, oocytes were hydrated and spawning occurred at dusk.

Evidence of multiple spawning was examined. Morphological and histological data showed that oocytes were continually recruited from March through the end of September, and the percentages of vitellogenic and fully yolked oocytes did not decline during the spawning season. An average of only 15.5% of the vitellogenic oocytes underwent FOM and hydration during a single spawn. Postovulatory follicles were found in many fish with mature ovaries throughout the reproductive season. Laboratory studies showed that this species is capable of repeated spawns. Batch fecundity was best predicted by ovary-free body weight of the fish and averaged 451 ± 43 eggs/g ovary-free body weight. Estimates of spawning frequency ranged from every other day to once every three weeks.

The spotted seatrout, *Cynoscion nebulosus*, supports important commercial and recreational fisheries throughout its range (Chesapeake Bay, Virginia to Tampico, Mexico; Tabb 1966). Whereas aspects of the reproductive biology of this sciaenid species have been documented throughout its range (i.e., Chesapeake Bay: Brown 1981; Georgia: Mahood 1975; Florida: Moody 1950, Klima and Tabb 1959, Tabb 1961; Mississippi: Overstreet 1983; Louisiana: Hein and Shepard 1979; Texas: Pearson 1929, Miles 1950, 1951), a comprehensive study of reproduction in spotted seatrout does not exist for any area. An extensive knowledge of the reproductive life history of a species is necessary to understand certain aspects of its reproductive physiology and endocrinology. Most previous studies have concentrated on the size at sexual maturity and the extended spawning season of this species (Pearson 1929; Moody 1950; Tabb 1961; Mahood 1975). A protracted spawning season is generally characteristic of multiple spawners (Nikolskii 1969). In addition, Overstreet's (1983) histological data suggest that *C. nebulosus* may be a multiple spawner. However, the possibility that spotted seatrout are multiple spawners has not been thoroughly discussed in the literature, and previous estimates of fecundity (Sundararaj and Suttkus 1962; Overstreet 1983) have not considered the multiple spawning nature of *C. nebulosus* or have included estimates of batch fecundity.

In the present study, the reproductive biology of *C. nebulosus* in South Texas was investigated, and particular attention was given to evidence for multiple spawning and estimates of batch fecundity and spawning frequency. The spawning season, spawning sites, time of spawning, and percentage of running ripe fish were documented. In addition, the temporal pattern of final oocyte maturation was determined. The histological appearance of the gonads was examined, and particular attention was given to the presence of postovulatory follicles in ovarian tissue, an indicator of multiple spawning in the northern anchovy, *Engraulis mordax* (Hunter and Goldberg 1980). The size-frequency distribution of vitellogenic oocytes was examined, since this can indicate multiple spawning (deVlaming 1983). Batch fecundity was determined and spawning frequency

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was estimated from both field-caught and laboratory fish.

MATERIALS AND METHODS

Collection of Samples

Spotted seatrout were collected in Redfish Bay or Lydia Ann Channel near Port Aransas, TX, U.S.A. at depths of 1–3 m (Fig. 1). Fish were captured using a 300 m gill net (82 mm stretch) or a 300 m trammel net (outer panels, 178 mm stretch; inner panel, 89 mm stretch) over shallow beds of turtle grass, *Thalassia testudinum* or shoal grass, *Halodule wrightii*, bordered by a 1–2 m drop-off into a channel. Fish <300 mm SL were captured with hook and line in 1–2 m of water.

Samples were collected weekly or twice monthly from March 1982 through early May 1985. No samples were taken in November and December 1983, October and December 1984, and February 1985. During 1982, samples were collected at dusk only; in 1983, 1984, and 1985, samples from dawn, midday, and midnight were also taken. During each sampling period, salinity and temperature were recorded as well as the time of capture.

Analysis of Fish and Gonads

Total length (TL) and standard length (SL) were measured to the nearest mm for each specimen and total body weight (WT) was determined to the nearest 10 g. Gonads were removed and weighed to the nearest 0.1 g (gonad weight, GW) and the gonadosomatic index (GSI) was calculated, using the formula: $GSI = (GW/WT) \times 100$.

Reproductive stage of the gonads was assessed macroscopically using the criteria in Table 1. The macroscopic criteria used were similar to those used by Overstreet (1983) and Macer (1974). A small portion of tissue was removed from the anterior or midsection of one gonad from each fish and preserved in Davidson's fixative for histological analysis (Jones 1966). Tissues were dehydrated and embedded in paraffin. Seven micron sections were cut and stained with Harris' hematoxylin and counterstained with eosin. Reproductive stage of each sample was assessed microscopically using the criteria in Table 1. Fish with

FIGURE 1.—Location of spotted seatrout sampling sites in South Texas. Asterisks denote sampling sites.

mature gonads were considered sexually mature. The microscopic criteria used were similar to those described by Yamamoto (1956), Hyder (1969), and Macer (1974). The percentages of each stage of oocyte, atretic structures, and postovulatory follicles were determined from histological slides of the ovaries of females >305 mm SL by counting all the oocytes in three randomly selected fields of view. An oocyte was counted if >50% of the cell was in the field of view. Two hundred and fifty to 500 oocytes were counted for each histological specimen.

A small portion of tissue (<0.5 g) was removed from the center of each ovary of females >305 mm SL collected in 1984 and 1985, placed in clearing solution (6 parts ethanol, 3 parts formalin, 1 part

TABLE 1.—Criteria used to describe gonadal reproductive stages of male and female spotted seatrout collected in South Texas.

Stage	Sex	Macroscopic appearance	Microscopic appearance
Immature	F	Ovary small, thin, light pink, slight vascularization. GSI range: 0.39–0.55.	Only primary oocytes present; no atretic oocytes. Lamellar margin thin.
	M	Testes small, thin, light grey, appearance similar to mesentery.	Only primary spermatogonia present.
Regressed	F	Ovary small, light pink, vascularization more obvious than in immature fish. GSI range: 0.39–1.16.	Primary chromatin nucleolar and early perinuceolar stage oocytes. Some atretic oocytes. Lamellar margin thicker than immature, more convoluted.
	M	Testes small, thin, white, slightly larger than immature fish. GSI range: 0.04–0.20.	Primary and secondary spermatogonia present.
Early developing	F	Ovary similar to regressed fish but slightly larger. GSI range: 0.80–1.26.	Appearance of late perinucleolar oocytes and primary cortical alveoli stage oocytes. No atretic oocytes present.
	M	Testes similar to regressed fish but slightly larger. GSI range: 0.16–0.48.	Many secondary spermatogonia and primary spermatocytes.
Developing	F	Ovary visably enlarged, light yellow, highly vascular, approximately 60% of the length of the body cavity. GSI range: 0.95–2.6.	Oocytes in secondary cortical alveolar stage and yolk granule stage. Many oocytes still in primary cortical alveolar stage. Early yolk globular stage present.
	M	Testes thickened, creamy white, no free milt expelled when cut. GSI range: 0.21–0.68.	All stages of spermatogenesis present, with few primary spermatogonia and free spermatozoa. Primary and secondary spermatocytes predominate.
Mature	F	Ovary large, brilliant yellow orange, oocytes visible to naked eye, vascularization prominent. Ovaries 80–90% length of body cavity. GSI range: 2.5–9.6.	Oocytes in yolk globular stage most common. Yolk and oil globules begin to encroach on nucleus. Largest oocytes range from 300 to 375 μm.
	M	Testes creamy white, thicker, more firm and elongated than developing testes. A small amount of milt expelled when cut. GSI range: 0.54–1.42.	No primary spermatogonia present, some secondary spermatogonia. Secondary spermatocytes and spermatids most numerous. Spermatozoa in central lobules.
Ripe	F	Oocytes hydrated, ovary looks clear, takes up almost entire body cavity, highly vascularized. GSI range: 12.5–19.9.	Many hydrated oocytes, irregularly shaped, eosinophilic. Other oocytes in yolk granular and yolk globular stages.
	M	Testes white, swollen, milt does not flow with light pressure, but flows freely when cut. GSI range: 1.07–1.62.	Spermatozoa, spermatids and secondary spermatocytes predominate. Few to no spermatogonia. Central lobules filled with spermatozoa.
Running ripe or spawning	F	Hydrated oocytes expelled with little to no pressure, ovary fluid, fills almost entire body cavity. GSI range: 7.7–17.6.	Same as ripe ovaries but fewer hydrated oocytes. Atretic and postovulatory follicles may be present.
	M	Testes creamy white, milt freely flowing with slight pressure. GSI range: 1.41–3.84.	Same as ripe fish, but spermatozoa evident in sperm ducts.
Partially spent	F	Ovary looks similar to mature condition but more flacid; occupies smaller percentage of body cavity. GSI range: 2.0–5.3.	Similar to mature ovary, except atretic oocytes in several stages of degeneration always evident. Postovulatory follicles occasionally present.
	M	Tests looks the same as running ripe but smaller. GSI range: 0.85–1.77.	No spermatogonia, few primary spermatoocytes. Most active spermatogenesis in peripheral lobules. Spermatozoa partially filling lobules and abundant in sperm ducts.
Spent	F	Ovary flacid but still highly vascularized, no longer than 50% of body cavity, pinkish in color. GSI range: 1.33–2.63.	Massive atresia of all remaining vitellogenic oocytes. Many primary and chromatin nucleolar oocytes present. Lamellar membrane highly convoluted.
	M	Testes flacid, width reduced, white. GSI range: 0.13–0.80.	Spermatozoa present in some lobules. Most lobules small, with only primary and secondary spermatogonia.

glacial acetic acid), and vigorously shaken for 30 seconds. Within a few minutes the cytoplasm cleared and the germinal vesicle could be easily observed microscopically. Ovarian fragments were taken from females collected at the spawning site over a 24-h period, placed in clearing solution and then examined under low-power magnification to determine the stage of final oocyte maturation.

Oocyte Size-Frequency Distributions and Estimates of Batch Fecundity

To determine fecundity and the frequency distribution of oocyte diameters, a 2–15 g piece of tissue was removed from the midsection of the ovaries of 57 fish and weighed to the nearest 0.01 g. The tissues were placed in a modified Gilson's solution (Bagenal 1966) for 3–12 months and periodically shaken to separate the oocytes from connective tissues. Ovaries containing hydrated oocytes were examined after three months since hydrated oocytes of spotted seatrout began to disintegrate when left in Gilson's solution for a longer period of time.

The volumetric method was used to estimate fecundity (Bagenal and Braum 1971). The oocyte samples were suspended in 500–1,500 mL of water and three replicate 0.5 or 1 mL subsamples were taken. All the oocytes >30 μm were counted, and those >80 μm in diameter (the growing oocytes) in each sample were measured to the nearest 15 μm using an ocular micrometer. A total of 556–1,110 growing oocytes were measured in each sample. The number of resting oocytes (oocyte diameter 30–80 μm) was determined by diluting the original oocyte suspension 1:10, and counting three replicate subsamples. Altogether, the frequency distributions of oocytes from 48 fish were analyzed (3 in developing stage; 9 in mature, spawning not imminent stage; 14 in mature, just prior to spawning stage; and 22 in running ripe stage). Fecundity was calculated following Macer's (1974) formula and expressed as relative fecundity of number of eggs per gram ovary-free body weight. Batch fecundity (BF) is defined as all oocytes >350 μm which were undergoing final oocyte maturation that formed a distinct batch, and all hydrated oocytes. This definition of batch fecundity is in agreement with Hunter and Macewicz's (1985) statement that oocytes undergoing final oocyte maturation may be included as hydrated oocytes when hydration occurs very rapidly.

Spawning of Fish in the Laboratory

Four female and two male spotted seatrout were maintained in a 30,000 L recirculating system. The tank, filtration system and feeding regime of the fish has been described previously (Arnold et al. 1976). The salinity ranged from 25 to 30‰. Spawning was induced by increasing the temperature and photoperiod from wintertime settings of 13°C, 9L:15D to 26°C and 15L:9D (Arnold et al. 1976). The filter boxes were checked daily for the presence of buoyant, newly fertilized eggs.

Statistical Analysis

Simple linear regression, oneway analysis of variance, and analysis of covariance were computed for the data using SPSS packaged programs (SPSS 1981).

RESULTS

Size at Maturity

Some female spotted seatrout were sexually mature after they reached 231 mm SL and >90% of the females had reached sexual maturity at 271 mm SL (Table 2). By 300 mm SL, all female spotted seatrout were sexually mature. Fish 300 mm SL or larger made up 85.4%, and immature fish comprised 6.5%, of all the females sampled.

Male spotted seatrout reached sexual maturity at a much smaller size than females. The size at

TABLE 2.—Number and percentage of mature female and male spotted seatrout by 10 mm size categories collected in South Texas, April 1982–May 1985. Maturity was judged by histological and macroscopic inspection.

Standard length (mm)	Female		Male	
	N	% mature	*N*	% mature
201–210	5	0	5	100
211–220	4	0	4	100
221–230	4	0	1	100
231–240	4	50	3	100
241–250	6	83	3	67
251–260	6	100	5	100
261–270	5	80	7	100
271–280	11	91	10	100
281–290	14	100	11	100
291–300	24	96	20	100
301–310	60	100	40	100
311–320	94	100	68	100
321–330	115	100	80	100
>330	945	100	507	100
Total	1,297		764	

which most male spotted seatrout attain sexual maturity could not be determined, since the smallest fish collected by the sampling methods (200 mm SL) were all sexually mature (Table 2).

Season and Time of Spawning

Histological and macroscopic examination of the gonads (see Table 3 and Figure 3) and mean GSI values (Fig. 2) show that spotted seatrout have an extended reproductive season in South Texas. Mean GSI values of males and females increased by April 1982–85 and remained elevated through the end of September. A 5°C increase in water temperature at the sampling sites to 23°C during the first week of April 1982–85 was paralleled by an increase in GSI to 2.1 in males and 4.5 or greater in females. The pattern of seasonal changes in mean GSI values of males was relatively consistent during the three-and-a-half years of sampling. Mean GSI values began to increase in mid-February, reached a maximum of 1.9–2.4 by April, and slowly declined during the spawning season until they dropped rapidly to regressed levels of 0.2 by the first half of October (Fig. 2). The seasonal patterns in mean GSI values of females were also similar from 1982 to 1985. In all four years, mean GSI increased in April and subsequently declined in May. In 1982–84, mean GSI increased again later in the season prior to the final decrease to regressed levels in October (Fig. 2). Thus, mean GSI values appear to be bimodal, with one period of peak spawning activity in April, and the second period of peak spawning activity varying between August 1982 and July 1983 and 1984.

Male and female spotted seatrout in spawning condition (males with freely flowing milt, females with ovulated oocytes) were consistently captured during a 2-h period around dusk over shallow (1 m) beds of *Thalassia testudinum* or *Halodule wrightii* bordered by a channel 2 m deep. The salinity at the spawning sites ranged from 20 to 37‰. Although actual spawning was not observed, collection of newly fertilized eggs from the spawning area at dusk confirmed that spawning was taking place (Holt and Holt[4]). Spawning fish were not captured over beds of scattered *H. wrightii* or *T. testudinum* that were not immediately adjacent to a channel. Females with freely

[4]S. A. Holt and G. J. Holt, University of Texas at Austin, Marine Science Institute, Port Aransas, TX 78373, pers. commun. 1983.

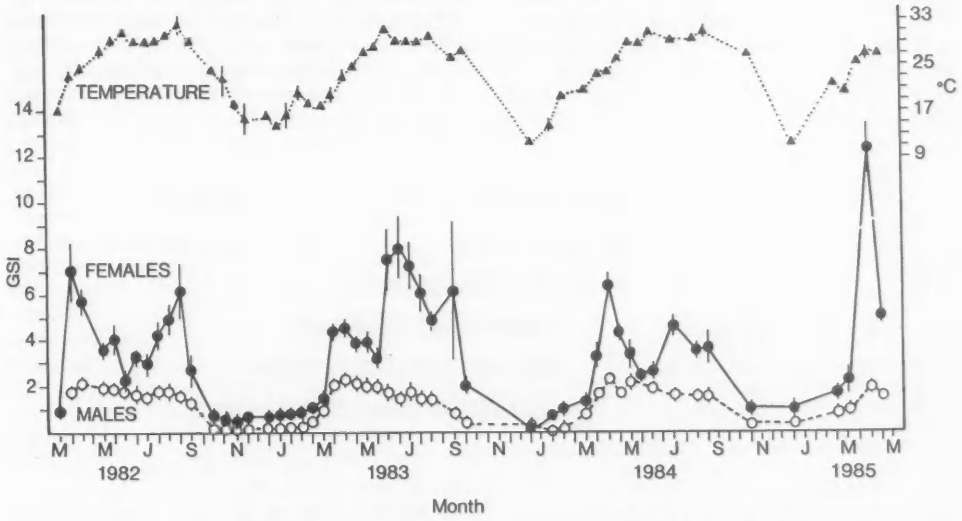

FIGURE 2.—Bi-monthly mean water temperature and mean gonadosomatic index (GSI) of male and female spotted seatrout collected in South Texas from March 1982 to May 1985, including ±1 SE of the mean. Sample size for each data point: 3–61 for females (sample size <15 in only 9 cases) and 2–52 for males (sample size <9 in only 9 cases).

flowing oocytes were only captured at dusk and milt appeared to flow more freely in males at dusk than at other times of the day.

Gonadal Development in Males

Testicular recrudescence began in January with the appearance of primary spermatocytes (Fig. 3), and by February the majority of the males were in the early developing or developing reproductive stage. In March, 89% of the males had testes containing free spermatozoa (Fig. 3), although only 27% were running ripe. Over 94% of all males captured from April until the end of August were running ripe. Spent males first appeared in August and all the males during October and November were either in the spent or regressed condition. In December, all males captured had regressed testes containing only primary and secondary spermatogonia (Fig. 3).

Histological observations revealed that the testes are the common unrestricted spermatogonia type, as described by Grier (1981). Spermatogenesis occurred throughout the entire testis during the majority of the year. However, from late February through early August, spermatogenesis was more advanced in the central lobules then in the peripheral lobules. By August there was no spermatogenic activity in the central lobules, although spermatogenesis continued in the peripheral lobules until mid-September. The only period of the year when there was no active spermatogenesis was from October through late January, although primary and secondary spermatogonia were present from October through the end of April (Fig. 3). Primary spermatocytes were common from late January until March, although they did not disappear from the testes entirely until the end of July. Secondary spermatocytes first appeared in mid-February, were common through the end of July and did not disappear until early September (Fig. 3). Spermatids and spermatozoa were present in the central lobules by late February, and from March through mid-August the central lobules were swollen with spermatozoa (Fig. 3). In late August and September many of the central lobules appeared to be partially empty of spermatozoa, although some spermatozoa were still present up to mid-November (Fig. 3). The peripheral lobules contained active spermatogenic cysts of primary and secondary spermatocytes during June and July and the lumens of these lobules began to fill with spermatozoa. The peripheral lobules were swollen with spermatozoa during August and September, but by mid-October no spermatozoa remained.

Gonadal Development in Females

Gonadal recrudescence was observed in a small percentage of the females captured in January and by March 94% of the females were undergoing ovarian development (Table 3). Fish with mature ovaries were found from March until the end of September, while running ripe fish were captured from April through the end of September (Table 3). Partially spent fish (females that appeared to have spawned at least once but still contained vitellogenic oocytes) were captured from May through the end of September. No com-

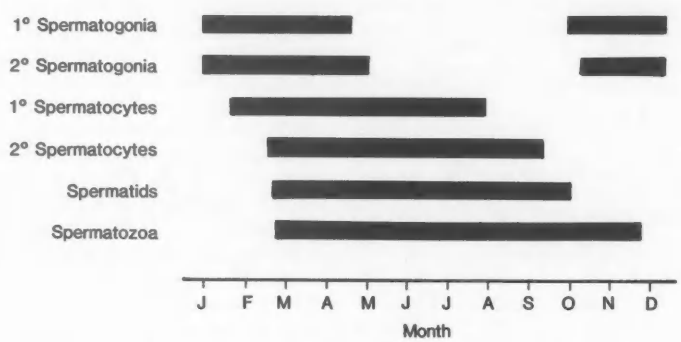

FIGURE 3.—Seasonal cycle of spermatogenesis in spotted seatrout collected in South Texas, as determined by histological and macroscopic observations. Data from April 1982 through mid-May 1985 are combined. 1° - primary, 2° - secondary.

TABLE 3.—Percentage of female spotted seatrout in seven reproductive stages by month, as assessed by histological and macroscopic examination of the ovaries. Data from April 1982 to May 1985 are combined. REG = Regressed, E DEV = Early Developing, DEV = Developing, MAT = Mature, RR = Ripe and Running Ripe, P SP = Partially Spent, SP = Spent.

		Percent in each reproductive stage						
Month	*N*	REG	E DEV	DEV	MAT	RR	P SP	SP
January	70	98	2					
February	51	55	43	2				
March	124	4	56	31	9			
April	372		4	6	78	12		
May	220			4	84	5	7	
June	104			1	56	19	24	
July	114		1		48	30	20	1
August	100				58	32	7	3
September	37	14			37	30	11	8
October	8	87						13
November	27	100						
December	51	98			2			
Total	1,278							

pletely spent fish were captured before July and few were captured during the remainder of the reproductive season.

Histological observations of fish with regressed ovaries collected from late September to mid-February showed only primary chromatin nucleolar and early perinucleolar oocytes. Atretic oocytes were present from September until mid-December; no atretic oocytes were observed from mid-December through the end of February. The appearance of late perinucleolar and primary cortical alveoli stage oocytes in late January, February, and early March represented the initial stages of ovarian recrudescence. Ovarian development was proceeding rapidly by early March and oocytes in the secondary cortical alveoli and yolk granule stages were common.

During the reproductive season, histological observations of the ovary showed a heterogeneous morphology. Oocytes in all stages of growth (from resting to the fully grown yolk globular stage) were distributed throughout the ovaries of all mature, running ripe, and partially spent fish collected from March through the end of September. Vitellogenesis was probably continuous from February until the end of September, as shown by the continual presence of large numbers of oocytes in the cortical alveoli and yolk granule stages. The relative percentages of three types of post cortical alveolar stage oocytes in fish in the mature reproductive stage did not change markedly from March through the end of September (Fig. 4). The percentage of oocytes in the yolk granule stage (diameter in histological preparations: 150–190 μm) varied from a low of 7.3% in June to a late season high of 16.1%, and averaged 13% of the total number of oocytes in the ovary. Yolk globular oocytes, the largest oocytes present (diameter: 200–375 μm), were most common. The percentage of oocytes in the yolk globular stage ranged from a high of 30.8% in April to an end-of-season low of 22.6% in September and averaged 26.9% during the reproductive season. In addition to the actively growing oocytes in the ovary, a small percentage of atretic oocytes was always found in fish with mature ovaries. Atretic oocytes are defined here as vitellogenic oocytes undergoing alpha stage atresia. The percentage of atretic oocytes ranged from a low of 2.2% in March to a midsummer high of 8% in July and averaged 5.4%. Additionally, postovulatory follicles (POF) were observed in the ovaries of fish captured from

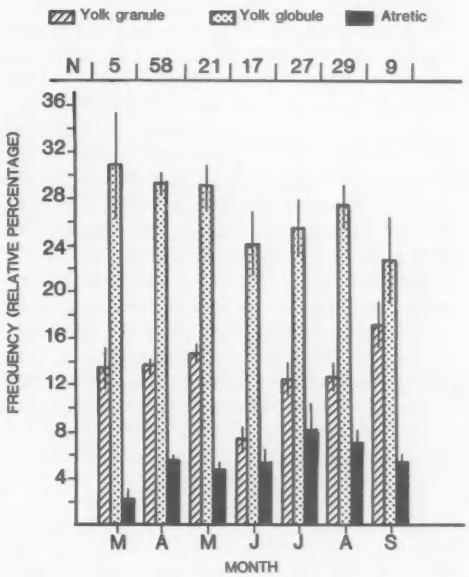

FIGURE 4.—Frequency of three different types of oocytes in female spotted seatrout ovaries in the mature reproductive stage (MAT, Table 3) as assessed by histological observation. Fish were collected from South Texas during the reproductive season. Frequency refers to the percentage of each type of oocyte relative to the total number of all types of oocytes counted. Data from April 1982 through the end of September 1983 are combined and the number (*N*) of individuals examined each month is indicated. Bars indicate mean percentage of oocytes ±1 SE of the mean. Yolk granule oocyte diameters ranged from 150 to 190 μm, and yolk globule oocyte diameters ranged from 200 to 375 μm in histological preparations. Atretic oocytes are defined here as oocytes in alpha stage atresia.

April through September, although the percentage of POF relative to the total number of oocytes was always small (<5%).

The histological appearance of the zona radiata and follicle layers changed as the oocytes developed. The zona radiata (chorion) was thin and nonstriated in perinucleolar and cortical alveoli oocytes. The zona radiata started to take on its characteristic striated appearance when oocytes reached the yolk granular stage and became noticeably thicker and more striated as oocytes grew into the yolk globular stage. In contrast, the granulosa and thecal layers appeared to decrease in thickness as oocyte development proceeded. Oocytes in the perinucleolar and cortical alveoli stages had thick, well-developed granulosa and thecal layers. In yolk granular and yolk globular oocytes, both follicle layers were noticeably thinner and the thecal layer was not always continuous around the oocyte.

Frequency distributions of growing oocytes (diameters in Gilson's solution >80 μm; perinucleolar to hydrated stage oocytes) from ovaries of 48 fish were analyzed, and Figure 5 shows typical patterns in fish from four reproductive stages. In a fish captured in March with developing ovaries, growing and vitellogenic oocytes (oocytes during the phase of active vitellogenin uptake) ranging from 80 to 185 μm in diameter were present (Fig. 5A; 625 oocytes counted). Fish in the mature reproductive stage in which spawning did not appear to be imminent, as indicated by GSI values <4, had growing and vitellogenic oocyte diameters ranging from 100 to 320 μm (Fig. 5B; 556 oocytes counted), comprising 21% of the total number of oocytes >30 μm in the ovary. Fish just prior to spawning, as indicated by GSI values >7, had a distinct batch of oocytes with diameters >350 μm that were undergoing final oocyte maturation (Fig. 5C; 585 oocytes counted). However, there were no other distinct modes of vitellogenic oocytes. In running ripe fish, the batch of large oocytes hydrated to a diameter of 520 μm or greater (Fig. 5D; 1,110 oocytes counted). The results (Figs. 5A–D) clearly demonstrate that *C. nebulosus* has a continuous distribution of growing and vitellogenic oocytes. The oocyte frequency distribution of the vitellogenic oocytes <320 μm in diameter remaining in running ripe fish ap-

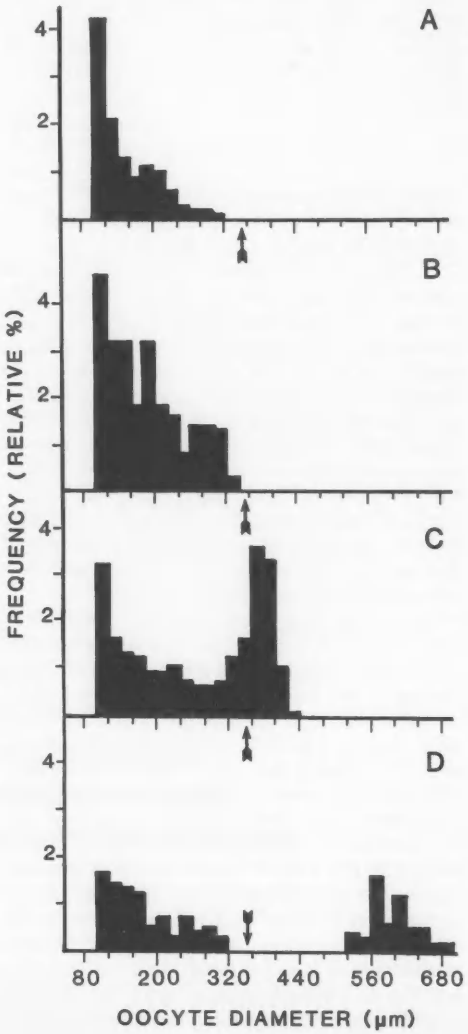

FIGURE 5.—Frequency distributions of growing oocyte diameters (>80 μm) in female spotted seatrout collected from South Texas. Growing oocytes comprised 21% of the total number of oocytes >30 μm in the ovary. Oocyte diameter refers to the diameters of oocytes after preservation in Gilson's solution. Frequency refers to the percentage of each size of oocyte relative to the total number of oocytes in the subsample. Each graph represents data from a single fish at a different reproductive stage. The arrow at 350 μm indicates the minimum size necessary for final maturation to occur. A. Developing stage in March, GSI = 1.6. B. Mature stage in which spawning is not imminent, GSI = 3.7. Fish in this stage were collected from April through the end of September. C. Mature stage just prior to spawning, GSI = 7.4. Fish in this stage were collected from April through the end of September. D. Running ripe stage, GSI = 17.6. Fish in this stage were collected from April through the end of September.

peared similar to the oocyte distribution in nonspawning fish (Fig. 5B, D). The percentage (21%) of growing and vitellogenic oocytes in the ovary remained constant throughout the reproductive season in fish in the mature and running ripe stages.

Final Oocyte Maturation

Final oocyte maturation (FOM) was highly synchronized in spotted seatrout and occurred only in oocytes >400 μm [5]. Figure 6A shows a photomicrograph of a histological section of a spotted seatrout ovary in the mature reproductive stage that was not undergoing final oocyte maturation. Many oocytes were in the yolk globular stage and appeared to be fully grown. The first readily observable stage of FOM in "cleared" oocytes was lipid coalescence (Fig. 6B). The oil droplets in the oocytes began to coalesce around the germinal vesicle (nucleus) and subsequently formed one to three large oil droplets. This stage was not always observed in histological preparations since many of the oocytes were not sectioned through their centers. The yolk globules remained discrete during lipid coalescence. After the lipids had coalesced, the germinal vesicle (GV) began to migrate to the periphery of the oocyte (germinal vesicle migration, or GVM). GVM could be seen in both histological sections (Fig. 6C) and in "cleared" oocytes (Fig. 6D). The oil droplet occupies the center of the oocytes shown in Figure 6C, D. Histological observation of this stage (Fig. 6C) showed that the yolk globules were not coalesced, the oil droplets had coalesced to form one or two large droplets and the GV had begun to lose its integrity and often appeared semicircular. At the completion of GVM, the nuclear (germinal vesicle) membrane broke down (GVBD) and the nuclear material intermingled with the cytoplasm of the oocyte. Hydration occurred shortly thereafter, followed by ovulation and spawning of the fully mature oocyte.

Final oocyte maturation occurred within 10 hours in spotted seatrout in the natural environment (Fig. 7). A total of 209 fish were collected over eight 24-h periods from April through August in 1984 and 1985. Forty-three percent of the fish collected between the hours of 0500 and 1500 were undergoing FOM. Lipid coalescence was first observed at dawn (0545), and GVM started at 0900. By 1430, all fish undergoing final maturation had hydrated oocytes and ovulation and spawning commenced at dusk (1830) and continued until 2100. None of the fish collected from 2100 to 0500 were undergoing FOM.

[5]A 400 μm live oocyte equals a 350 μm oocyte preserved in Gilson's solution. Both measurements represent oocytes beginning FOM.

Batch Fecundity

The significant positive relationship ($P < 0.001$) between BF and ovary-free body weight can be best described by the following equation: $BF = 459WT - 56{,}066$, $r^2 = 0.56$ (Fig. 8), while curvilinear equations best described the relationship between BF and SL and TL. The coefficients of determination in all cases were <0.56.

A one-way analysis of variance showed that mean BF (number of eggs per gram ovary-free weight) did not vary significantly during the April through September spawning season. Mean relative batch fecundity was highest in September, lowest in May, and varied little during April, June, and July (Table 4).

A prominent batch of oocytes was present only in females that were in all stages of final oocyte maturation or were running ripe (Figs. 5C, D; 7). The average batch size calculated from 14 fish containing hydrated oocytes and no postovulatory follicles was 451 ± 43 eggs/g ovary-free body weight. This number averaged 15.5 ± 2.5% of the number of growing and vitellogenic oocytes in the ovary.

TABLE 4.—Monthly mean batch fecundity expressed as number eggs/g ovary-free body weight of spotted seatrout in South Texas. All means were not statistically different.

Month	N	Mean fecundity ±1 SE
April	19	477 ± 42
May	2	320 ± 72
June	3	435 ± 109
July	5	409 ± 76
August	3	361 ± 60
September	3	560 ± 79

Spawning Frequency

To estimate the spawning frequency of spotted seatrout in South Texas, the percentage of running ripe females captured monthly from April through the end of September in 1982 through 1985 was examined. Only fish captured at dusk and >305 mm SL were included in this analysis. The percentage of spawning females ranged from

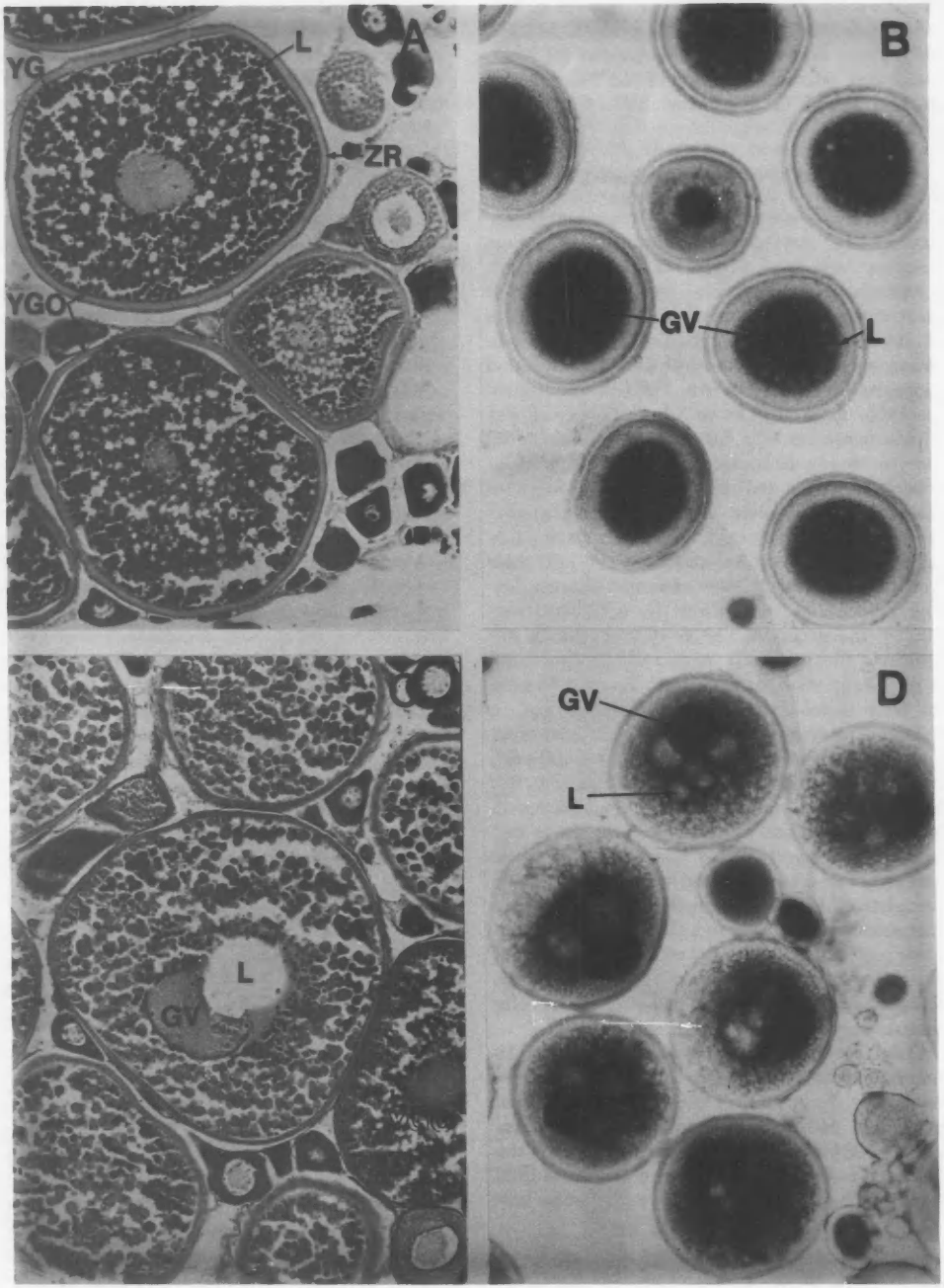
A
L
YG
ZR
YGO
B
GV
L
C
L
GV
D
GV
L

FIGURE 6.—Photomicrographs of oocytes from spotted seatrout in the mature reproductive stage collected from South Texas. A. Histological section of an ovary in the mature stage that is not undergoing final oocyte maturation (FOM). Oocyte development is continuous, with fully grown yolk globular oocytes co-occurring with oocytes in earlier stages of development (Magnification 120×). B. "Cleared" oocytes in the lipid coalescence stage, the first stage of FOM (magnification 40×). C. Histological section of an oocyte undergoing germinal vesicle migration (GVM). (Magnification 160×). D. "Cleared" oocytes in the GVM stage (magnification 40×). Key: GV = germinal vesicle or nucleus, L = Lipid droplets, YG = yolk globules, YGO = yolk globular oocyte, ZR = Zona radiata.

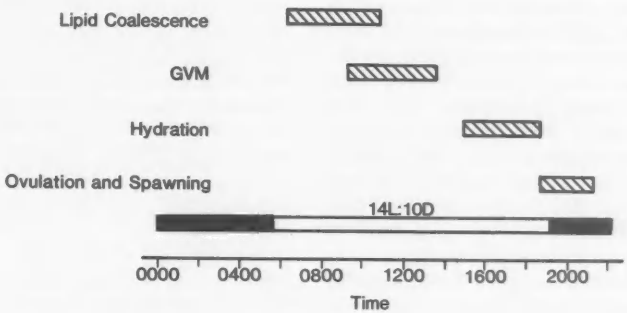

FIGURE 7.—Time-course of final oocyte maturation in spotted seatrout collected from South Texas. Lipid coalescence is the initial stage in final oocyte maturation. Data obtained from 46 fish undergoing final oocyte maturation in April and May 1985. GVM = germinal vesicle migration. 14L: 10D = hours of light and dark.

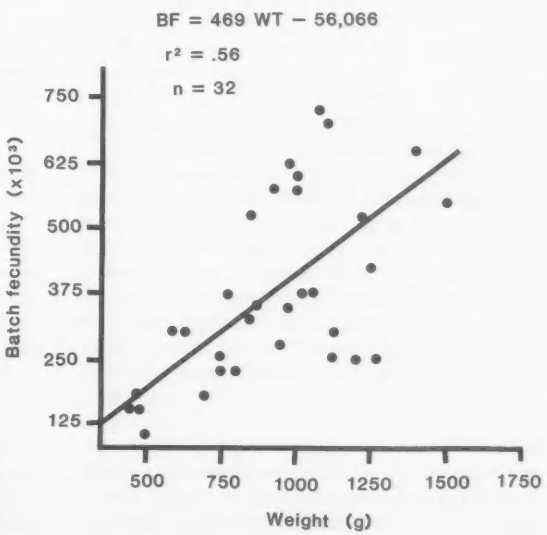

FIGURE 8.—Relation between batch fecundity (BF) and ovary-free body weight (WT) of spotted seatrout from April 1984 to May 1985. Thirty-three fish with oocytes >350 μm that were undergoing final oocyte maturation and formed a distinct batch of oocytes or had hydrated oocytes are included.

a low of 8% in May to a high of 45% in September (Table 5). An average of 27.5% of the females captured during the spawning season were running ripe, corresponding to an average spawning frequency of once every 3.6 days or 50 times during the 6-mo spawning period.

The spawning frequency was also estimated from females that were undergoing final oocyte maturation (FOM) between the hours of 0600 and 1400 in April, May, July, and August 1984 and 1985 (Table 5). For comparison, the actual percentage of running ripe females captured during the same months is also presented. An average of 42.8% of the females examined for final oocyte maturation from April through August were undergoing FOM. Therefore, average spawning frequency was once every 2.3 days, or 80 times during the 6-mo spawning season.

Spawning frequency was also estimated from the percentage of females captured with ovaries containing postovulatory follicles (POF). An average of 13.1% of the females captured had ovaries which contained POF ranging from 12 hours to 2 days old. This would correspond to a spawning frequency of once every 7.6 days or 24 times during the spawning season.

Finally, the spawning frequency of four female *C. nebulosus* in the laboratory under conditions of controlled temperature and photoperiod were examined (Table 6). The fish spawned from 1 to 10 times each month for 17 months, an average of 17 spawns per individual over a 12-mo period (Table 6). This would correspond to a spawning frequency of once every 21 days.

TABLE 5.—Percentage of spotted seatrout spawning (RR) or undergoing final oocyte maturation (FOM) in South Texas. Data on spawning fish collected April 1982–May 1985. Data on fish undergoing FOM collected April 1984–May 1985.

	Spawning fish 1982–85			Fish undergoing FOM 1984–85			
Month	*N*	# RR	% RR	*N*	# FOM	% FOM	% RR
April	256	42	16	33	14	42	37
May	140	11	8	21	10	48	13
June	101	20	20	—	—	—	—
July	82	33	40	7	3	43	52
August	101	36	36	8	3	38	—
September	20	9	45	—	—	—	—
Mean			27.5			42.8	25.5

TABLE 6.—Number of spawns and average water temperature by month for four female spotted seatrout contained in a 30,000 L tank in Port Aransas, TX, under conditions of controlled temperature and photoperiod, July 1974–November 1975. Experimental procedures described in Arnold et al. (1976).

Month	Number of spawns	°C
July	8	26.75
August	7	26.75
September	4	26.0
October	6	25.5
November	4	24.5
December	8	24.0
January	9	23.5
February	10	24.0
March	10	24.0
April	3	25.75
May	1	25.0
June	0	22.0
July	6	25.75
August	2	25.0
September	2	23.0
October	9	23.5
November	10	24.0
Total	99	
Average:	17 spawns/ 12 months/ female	

DISCUSSION

Sexual Maturity and Spawning Season

Male spotted seatrout reached sexual maturity at a smaller size than females which appears to be a fairly common phenomenon in spotted seatrout throughout its range (see Mercer 1984 for a review). Both male and female spotted seatrout in South Texas reached sexual maturity at a size similar to that reported for other groups of *C. nebulosus* along the Gulf Coast (Moody 1950; Klima and Tabb 1959; Overstreet 1983) and at a smaller size than along the East Coast (Tabb 1961; Brown 1981).

Running ripe females were captured only between one hour before and two hours after sunset in South Texas, suggesting a high degree of synchrony in spawning fish. Collections of newly fertilized eggs during a $2\frac{1}{2}$-h period after sunset (Holt et al. 1985) provides supporting evidence for this spawning synchrony.

Both histological data and GSI values showed spotted seatrout have an extended spawning season in South Texas. Gonadal recrudescence began in January in male and in February in female spotted seatrout. Spawning commenced in April and continued until the end of September. Other studies of *C. nebulosus* along the Gulf and East coasts of the United States have also reported long spawning seasons (Mercer 1984). Additionally, other sciaenids have extended spawning seasons (Merriner 1976; White and Chittenden 1977; DeVries and Chittenden 1982; Love et al. 1984),

suggesting a prolonged spawning season is a common reproductive strategy among sciaenids living in temperate and subtropical waters.

The duration of the spawning season may be related to water temperature. Perhaps this apparent association with temperature is related to the viability and development of spawned spotted seatrout eggs. Twenty-three degrees may be the minimum temperature necessary for successful spawning, as indicated by both the failure to capture running ripe fish at lower temperatures and by data from spotted seatrout induced to spawn under laboratory conditions (Arnold et al. 1976; Table 6). However, since spawning ceased in September when water temperatures were well above 23°C, possibly a decrease in photoperiod in combination with a decrease in temperature provides the necessary cue for termination of spawning. Hein and Shepard (1979) suggested photoperiod may be an important regulating factor in *C. nebulosus* spawning. Data from laboratory-spawned spotted seatrout (Arnold et al. 1976) also support this speculation.

The seasonal pattern of mean GSI values during the spawning season was relatively consistent for both males and females over the $3\frac{1}{2}$-yr period, 1982–85 (Fig. 2). The bimodality of the female GSI data suggests the possibility of two peaks in spawning activity, although the timing of the second peak varies from year to year, thus demonstrating the need for several consecutive years of data. Bimodal spawning peaks have been previously reported for the species by Hein and Shepard (1979) in Louisiana, Stewart (1961) in Florida, and Brown (1981) in Chesapeake Bay, VA. However, mean GSI values should be used with caution when attempting to predict actual peaks in spawning activity (deVlaming et al. 1982).

Fecundity

Accurate annual fecundity measurements are difficult to determine for multiple spawning fishes with an extended spawning season. Methods of calculating annual fecundity from measurements of the total number of growing oocytes at the beginning of the spawning season (Bagenal 1966), or other approaches based on the total number of oocytes at the beginning of the spawning season minus egg retention at the end of the spawning season (Conover 1985), are inappropriate for multiple spawning species such as spotted seatrout which show continuous recruitment of oocytes during the reproductive season. Thus, the previous estimates of annual fecundity in spotted seatrout, which did not take continuous recruitment of oocytes into consideration and measured either total fecundity (Overstreet 1983) or fecundity of growing and vitellogenic oocytes (Sundararaj and Suttkus 1962), probably underestimated annual fecundity. Furthermore, BF has not previously been calculated for this species.

Although no monthly differences in BF were apparent (Table 4), sample sizes were too small to draw any definite conclusions from these data. The relatively low coefficient of determination (0.56) is similar to values reported by Conover (1985) for Atlantic silversides, *Menidia menidia*, another multiple spawning species. Perhaps a more accurate estimate of annual fecundity than previously reported for spotted seatrout can be obtained by multiplying BF by the number of spawns during the reproductive season. Unfortunately, as discussed later, estimates of spawning frequency vary considerably, so it is not possible to make an accurate estimation of the annual fecundity. However, available data indicate that average annual fecundity may be greater than 10 million eggs.

Multiple Spawning

Histological examination of the testes revealed that spermatogenesis ceased earlier in the central lobules, although they contained spermatozoa one-and-one-half months longer than the peripheral lobules. It is possible that the same central lobules act as storage areas for spermatozoa produced by the more spermatogenically active peripheral lobules during the second half of the spawning season, as suggested by Hyder (1969) for *Tilapia*. This may represent a strategy in multiple spawning fish with a prolonged spawning season that allows for a constant supply of spermatozoa while investing a minimal amount of energy into spermatogenesis.

Several lines of evidence indicate that female *C. nebulosus* also spawn several times during the reproductive season. The relatively high percentage of running ripe females, fish undergoing FOM and partially spent fish captured throughout the spawning season, and the absence of completely spent fish until the last third of the spawning season, suggest that an individual does not spawn all the vitellogenic eggs in the ovary at one time. Indeed, oocyte size-frequency analysis shows a continuous distribution of growing and

vitellogenic oocytes (Fig. 5) and fecundity estimates show that only about 15% of the growing oocytes undergo FOM prior to a spawn. Histological data shows that the percentage of vitellogenic oocytes in the ovary remains constant throughout the spawning season (Fig. 4), which suggests that new oocytes may be recruited into the vitellogenic phase as rapidly as mature oocytes are released. Convincing histological evidence of multiple spawning is the presence of postovulatory follicles (POF) from May through the end of September in ovaries containing many vitellogenic oocytes. Hunter and Goldberg (1980) characterized postovulatory follicles in laboratory-spawned *Engraulis mordax*, a multiple spawning fish, and found POF in all females that had spawned in the laboratory one or two days previously. Finally, laboratory studies also show that spotted seatrout are capable of multiple spawning under relatively constant environmental conditions (Table 6). Tucker and Faulkner (1987) also found that six female fish kept in raceways outdoors at the ambient summer temperature and photoperiod spawned repeatedly.

Spawning Frequency

It is especially difficult to determine the spawning frequency of wide-ranging, multiple-spawning marine fishes such as *C. nebulosus* that are not group-synchronous spawners. One method to estimate spawning frequency is to count the number of distinct batches of vitellogenic oocytes in the ovary (Shackley and King 1977). However, only one distinct batch of vitellogenic or hydrated oocytes can be distinguished in spotted seatrout ovaries at any one time (Fig. 5) and the reliability of this method has been questioned (deVlaming 1983). Therefore, three techniques were used to estimate spawning frequency in spotted seatrout.

Spawning frequency was estimated to be once every 3.6 days from the percentage of running ripe fish caught on the spawning grounds. Although this is probably an overestimate owing to sampling bias, the error may not be susbtantial, since the spawning grounds are also the feeding grounds for this species (Moody 1950) and many nonspawning individuals were captured. The time of sample collection did not significantly influence the estimate of spawning frequency. High spawning frequencies were also obtained (every 2.3 days) when fish were captured 6–12 hours prior to spawning and examined for signs of final oocyte maturation (Table 5). The spawning frequency of other sciaenids fishes has been estimated by this technique (DeMartini and Fountain 1981; Love et al. 1984). Additionally, Hunter and Macewicz (1985) suggested that this method produces a useful first approximation of spawning frequency.

The proportion of fish having POF in the ovary has also been used to determine spawning frequency (Hunter and Goldberg 1980; Alheit et al. 1984; Hunter and Macewicz 1985). Spotted seatrout were found to have POF throughout the spawning season, although the age of the POF was often difficult to determine. Furthermore, detailed laboratory studies have not been undertaken to accurately age POF in spotted seatrout. However, the once a week estimate of spawning frequency obtained using this method is similar to spawning frequencies reported for two other sciaenids, the queenfish, *Seriphus politus*, (DeMartini and Fountain 1981) and the white croaker, *Genyonemus lineatus*, (Love et al. 1984). Spawing frequency estimates from POF are probably more reliable than estimates based on the number of spawning fish since sampling bias is less likely to occur when capturing fish with POF.

Another method used to quantify spawning frequencies in various species is direct observation of spawning in the laboratory or in "controlled" field situations, such as impoundments (Gale and Deutsch 1985; Hubbs 1985; Heins and Rabito 1986). Spotted seatrout spawned an average of once every three weeks per individual under controlled temperature and photoperiod in the laboratory (Table 6). Tucker and Faulkner (1987) found that six female spotted seatrout kept outdoors at ambient temperature and photoperiod averaged one spawn per individual every 2.3 weeks. The same spawning frequency was noted for an individual female, although that same individual later spawned three times in four days (Tucker and Faulkner 1987). Thus, spotted seatrout appear to be capable of the high spawning frequencies estimated from field-caught fish with hydrated ovaries, although this frequency is probably not sustained throughout the entire spawning season. In general, the spawning frequencies in both laboratory studies are lower than those estimated from actual spawning fish in the field. However, it is unclear whether this is due to an overestimation of spawning frequency in the field or to a decline in spawning frequency owing to confinement in the laboratory.

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LITERATURE CITED

ALHEIT, J., V. H. ALARON, AND B. J. MACEWICZ.
1984. Spawning frequency and sex ratio in the peruvian anchovy, *Engraulis ringens*. CalCOFI. Rep. 25:43–52.

ARNOLD, C. R., T. D. WILLIAMS, W. A. FABLE, JR., J. L. LASSWELL, AND W. H. BAILEY.
1976. Methods and techniques for spawning and rearing spotted seatrout (*Cynoscion nebulosus*) in the laboratory. Proc. 30th Conf. Southeast. Assoc. Game Fish Comm. 30:167–178.

BAGENAL, T. B.
1966. The ecological and geographical aspects of the fecundity of the plaice. J. Mar. Biol. Assoc. U.K. 46:161–186.

BAGENAL, T. B., AND E. BRAUM.
1971. Eggs and early life history. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p 159–181. IBP (Int. Biol. Prgramme). Handb. 3, 2d ed., Blackwell Sci. Publ. Oxford, England.

BROWN, N. J.
1981. Reproductive biology and recreational fishery for spotted seatrout, *Cynoscion nebulosus*, in the Chesapeake Bay area. MA Thesis, College of William and Mary, Gloucester Point, VA, 120 p.

CONOVER, D. O.
1985. Field and laboratory assessment of patterns in fecundity of a multiple spawning fish: The Atlantic silverside, *Menidia menidia*. Fish. Bull., US. 83:331–341.

DEMARTINI, E. E., AND R. K. FOUNTAIN.
1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. Fish. Bull., U.S. 79:547–560.

DEVLAMING, V.
1983. Oocyte development patterns and hormonal involvements among teleosts. *In* J. C. Rankin, T. J. Pitcher, and R. T. Duggan (editors), Control processes in fish physiology, p. 176–199. Wiley & Sons, N.Y.

DEVLAMING, V., G. GROSSMAN, AND F. CHAPMAN.
1982. On the use of the gonosomatic index. Comp. Biochem. Physiol. 73A:31–39.

DEVRIES, D. A., AND M. E. CHITTENDEN, JR.
1982. Spawning, age determination, longevity and mortality of the silver seatrout, *Cynoscion nothus*, in the Gulf of Mexico. Fish. Bull., U.S. 80:487–500.

GALE, W. F., AND W. G. DEUTSCH.
1985. Fecundity and spawning frequency of captive tesselated darters - fractional spawners. Trans. Am. Fish. Soc. 114:220–229.

GRIER, H. J.
1981. Cellular organization of the testis and spermatogenesis in fishes. Am. Zool. 21:345–357.

HEIN, S., AND J. SHEPARD.
1979. Spawning of spotted seatrout in a Louisiana estuarine ecosystem. Proc. Annu. Conf. Southeast. Assoc. Fish. Wildl. Agencies 33:451–465.

HEINS, D. L., AND F. G. RABITO, JR.
1986. Spawning performance in North American minnows: Direct evidence of the occurrence of multiple clutches in the genus *Notropis*. J. Fish Biol. 28:343–357.

HOLT, G. J., S. A. HOLT, AND C. R. ARNOLD.
1985. Diel periodicity of spawning in sciaenids. Mar. Ecol. Prog. Ser. 27:1–7.

HUBBS, C.
1985. Darter reproductive season. Copeia 1985:56–68.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641–652.

HUNTER J. R., AND B. J. MACEWICZ.
1985. Measurement of spawning frequency in multiple spawning fishes. *In* R. Lasker (editor), An egg production method for estimation spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, p. 79-94. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

HYDER, M.
1969. Histological studies on the testis of *Tilapia leucosticta* and other species of the genus *Tilapia* (Pisces: Teleostei). Trans. Am. Microsc. Soc. 88:211–231.

JONES, R. MCC.
1966. Basic microscopic techniques. 5th ed. Chicago Univ. Press. (See p. 249).

KLIMA, E. F., AND D. C. TABB.
1959. A contribution to the biology of the spotted weakfish *Cynoscion nebulosus* from northwest Florida, with a description of the fishery. Fla. State Board Conserv. Tech. Ser. 30, 24 p.

LOVE, M. S., G. E. MCGOWEN, W. WESTPHAL, R. J. LAVENBERG, AND L. MARTIN.
1984. Aspects of the life history and fishery of the white croaker, *Genyonemus lineatus* (Sciaenidae), off California. Fish. Bull., U.S. 82:179–198.

MACER, C. T.
1974. The reproductive biology of the horse mackerel, *Trachurus trachurus* (L.) in the North Sea and English Channel. J. Fish Biol. 6:415–438.

MAHOOD, R. K.
1975. Spotted seatrout in coastal waters of Georgia. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 29:195–207.

MERCER, L. P.
1984. A biological and fisheries profile of spotted seatrout, *Cynoscion nebulosus*. N.C. Dep. Nat. Res. Comm. Dev. Div. Mar. Fish., Spec. Sci. Rep. No. 40, 87 p.

MERRINER, J. V.
1976. Aspects of the reproductive biology of the weakfish, *Cynoscion regalis* (Sciaenidae), in North Carolina. Fish. Bull., U.S. 74:18–26.

MILES, D. W.
1950. The life histories of the spotted seatrout, *Cynoscion nebulosus* and the redfish, *Sciaenops ocellatus*. Tex. Game Fish Comm. Mar. Lab. Annu. Rep. 1949–1950, 38 p.
1951. The life histories of the seatrout, *Cynoscion nebulosus*, and the redfish, *Sciaenops ocellatus*: Sexual development. Tex. Game Fish Comm. Mar. Lab. Annu. Rep. 1950-1951, 11 p.

MOODY, W. D.
1950. A study of the natural history of the spotted seatrout, *Cynoscion nebulosus*, in the Cedar Key, Florida area. Q. J. Fla. Acad. Sci. 12:147–172.

NIKOLSKII, G. V.
1969. Theory of fish population dynamics as the biological background for rational exploitation and management of fishery resources. Oliver & Boyd, Edinb., 323 p.

OVERSTREET, R. M.
1983. Aspects of the biology of the spotted seatrout, *Cynoscion nebulosus*, in Mississippi. Gulf Res. Rep. Suppl. 1:1–43.

PEARSON, J. C.
1929. Natural history and conservation of redfish and other commercial Sciaenids on the Texas coast. Bull. U.S. Bur. Fish. 44:129–214.

SHACKLEY, S. E., AND P. E. KING.
1977. The reproductive cycle and its control; frequency of spawning and fecundity in *Blennius pholis* L. J. Exp. Mar. Biol. Ecol. 30:73–83.

SPSS INC.
1981. SPSS user's guide. 2d ed. SPSS, Inc., 988 p.

STEWART, K. W.
1961. Contributions to the biology of the spotted seatrout (*Cynoscion nebulosus*) in the Everglades National Park, Florida. M.S. Thesis, Univ. Miami, Coral Gables, FL, 103 p.

SUNDARARAJ, B. I., AND R. D. SUTTKUS.
1962. Fecundity of the spotted seatrout *Cynoscion nebulosus* (Cuvier) from Lake Borgne area, LA. Trans. Am. Fish. Soc. 91:84–88.

TABB, D. C.
1961. A contribution to the biology of the spotted seatrout, *Cynoscion nebulosus* of East Central Florida. Fla. State Board Conserv. Tech. Ser. 35, 21 p.
1966. The estuary as a habitat for spotted seatrout, *Cynoscion nebulosus*. Am. Fish. Soc. Spec. Publ. 3:59–67.

TUCKER, J. W., JR., AND B. E. FAULKNER.
1987. Voluntary spawning patterns of captive spotted seatrout. Northeast Gulf Sci. 9:59–63.

WHITE, M. L., AND M. E. CHITTENDEN, JR.
1977. Age determination, reproduction and population dynamics of the Atlantic croaker, *Micropogonias undulatus*. Fish. Bull., U.S. 75:109–123.

YAMAMOTO, N.
1956. Studies on the formation of fish eggs. I. Annual cycle in the development of ovarian eggs in the flounder, *Liopsetta obscura*. J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool. 12:362–373.

NOTES ON REPRODUCTION IN THE SCALLOPED HAMMERHEAD, *SPHYRNA LEWINI*, IN NORTHEASTERN TAIWAN WATERS

The reproductive mode of hammerhead sharks (family Sphyrnidae) is placental viviparity, following Teshima's (1981) designations. Three species of hammerhead sharks are known from northeastern Taiwanese waters: *Sphyrna lewini* (Griffith and Smith), *S. mokarran* (Rüppel), and *S. zygaena* (Linnaeus). The scalloped hammerhead, *S. lewini*, commonly found from Pung-Chia Island to Guei-Shan Island (Fig. 1) is one of the most abundant shark species in this area. Based on data from the Nan Fan Ao Fish Market (located in northeastern Taiwan), 460–510 t/year from 1982 through 1984 were landed, representing one-fourth of the total catches of sharks in this area (the total landing being 1,760–2,240 t/year). Catches peaked in spring and winter and were lower in summer and autumn.

This species is also distributed in western and southern waters of Taiwan; however, the catch from those areas were smaller. The employees of the southern and western fish markets explained that the scalloped hammerhead is occasionally seen in small numbers in those areas, but there are no landing data. It is also common in coastal warm temperate and tropical seas throughout much of the world (Compagno 1984). Although

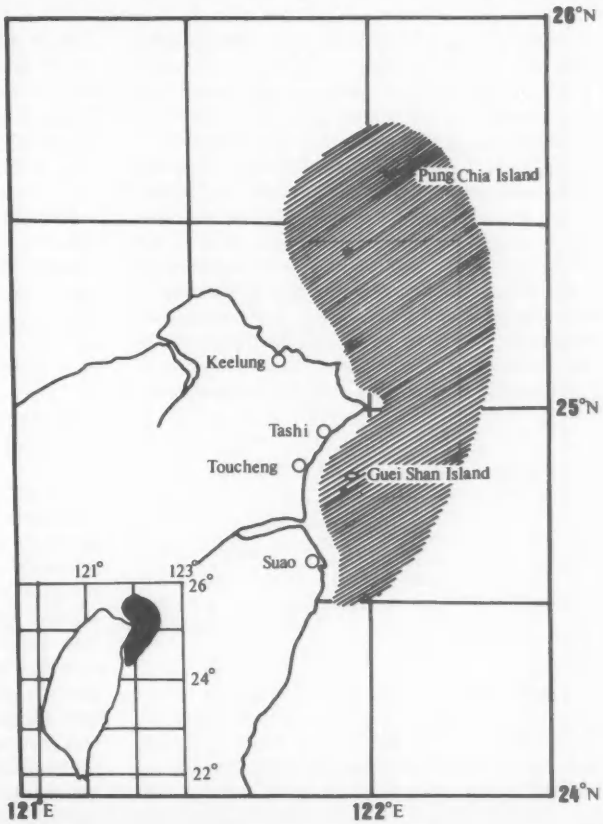

FIGURE 1.—Sampling area of *Sphyrna lewini*.

the scalloped hammerhead is one of the most valuable food resources in Taiwan, many facets of its life history, particularly reproduction, are not well known. This study provides information about certain aspects of reproduction in the scalloped hammerhead in northeastern Taiwan waters.

Materials and Methods

From September 1982 to June 1983 and from December 1983 to September 1985, shark specimens were examined and material collected monthly at Nan Fan Ao Fish Market. These sharks had been caught by drift longlines set near the surface to around 100 m, or by surface harpoon. A total of 674 scalloped hammerhead sharks were examined at the fish market (Table 1). Data recorded included total length measured from the tip of the snout to the tip of the upper lobe of the caudal fin (straight line measure), body weight, clasper length (measured from cloaca to the tip of claspers), ovarian egg diameter and number, and condition of the uteri. In addition, uterine embryos were counted, sexed, and measured for total length. Counts of litter size included any uterine eggs as well as embryos.

Stages of maturity for both females and males were categorized simply as "mature" or "immature". Females having threadlike uteri and tiny ovarian eggs were called immature, while those with eggs larger than 25 mm in diameter, with uteri containing embryos or eggs or with empty but expanded and flaccid uteri, were designated as mature. Males with rigid claspers were classified as being mature. Clasper length relative to total length also gave an indication of maturity.

TABLE 1.—The number of specimens examined in this study.

	Number of specimens			
	Immature		Mature	
Month	Male	Female	Male	Female
Jan.	13	11	18	93
Feb.	3	3	17	43
Mar.	4	13	4	44
Apr.	8	34	16	68
May	3	6	9	33
June	3	2	4	20
July	4	3	11	60
Aug.	3	1	6	19
Sept.	0	7	3	15
Oct.	0	1	1	3
Nov.	0	6	1	38
Dec.	1	8	1	10
Total	42	95	91	446

Results

The reproductive organs of scalloped hammerhead closely resemble those of the bonnethead shark, *S. tiburo* (described by Schlernitzauer and Gilbert 1966).

As with the bonnethead shark, only the right ovary of the scalloped hammerhead is functional, supplying both oviducts. As the ovarian eggs mature (>25 mm diameter), they pass through the common ostium into the oviducts, where they are fertilized. The eggs then become encased in the embryonic membrane as they pass through the nidamental gland and descend into the uterus. In the uterus, embryonic development proceeds, nourished by a yolk sac. After a period, the uterine compartments develop, which enclose the embryo, and a yolk-sac placenta is implanted. After the yolk is exhausted, the embryo is nourished until birth by the placenta through the umbilical stalk.

Based on the condition of the uterus and ovary, female scalloped hammerheads became mature at a larger size, around 210 cm, than males. All females over 230 cm were mature.

Based on the rigidity of the claspers, male scalloped hammerheads reached their first maturity at a total length of 198 cm, while all those over 210 cm were mature.

The clasper length of males increases rapidly relative to total length, until the sharks reach around 200 cm, at which size the clasper length/total length relationship plateaus, suggesting that sexual maturity has been attained (Fig. 2). Also, this size marked the approximate transition point from flaccid to rigid claspers (Fig. 2).

It takes roughly 10 months of development from egg formation to ovulation (Fig. 3). In October and November, eggs were very small, measuring about 2 mm in diameter. By July they had increased in size to about 30–38 mm and numbered 40–50 per female, and by August and September they had grown to about 40–45 mm. In one mature female, in September we counted 28 uterine eggs and 4 ovarian ones measuring 45 mm in diameter. This suggested that the 4 ovarian eggs were ready for ovulation. Because ovarian eggs larger than 30 mm in diameter seemed near ovulation, we concluded that ovulation occurred between July and October.

The parturition season lasts from May to July, and the gestation period of this species was estimated to be roughly 10 months (Fig. 4). No em-

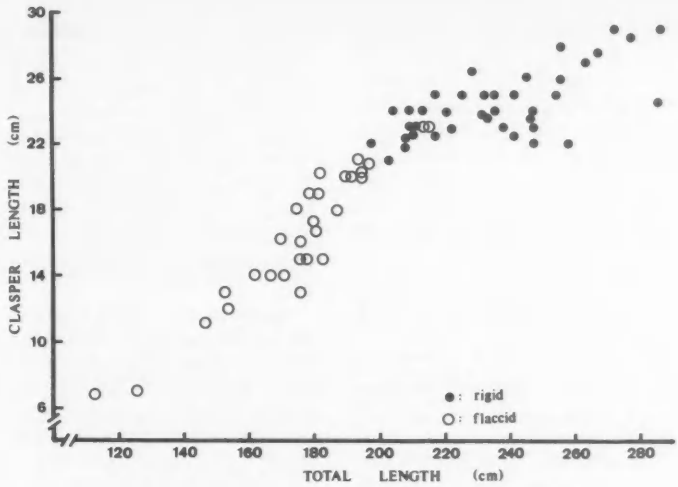

FIGURE 2.—Relationship between total length and clasper length in *Sphyrna lewini*.

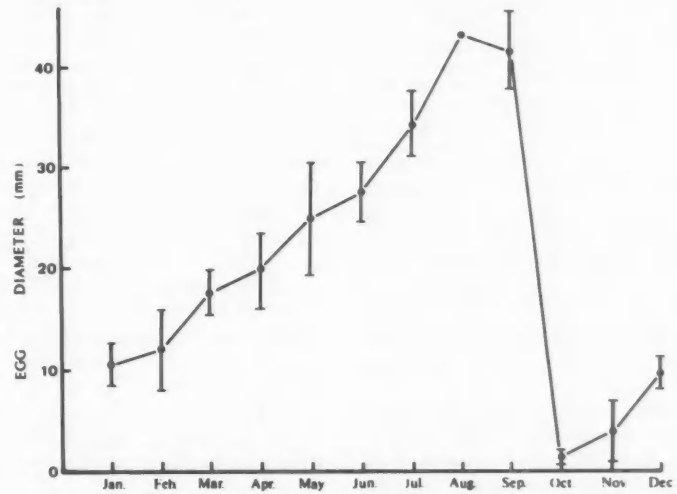

FIGURE 3.—Monthly increase in the ovarian egg diameter of *Sphyrna lewini*. Error bars represent 2 SD; numerals, sample size.

bryos were found in July and August, though some mature sharks had large ovarian eggs measuring about 30–40 mm in diameter during those months. The first uterine eggs, and embryos measuring around 2 cm were found in September. Uterine eggs were observed until November. After nine more months of rapid growth, the embryos attained a total length of around 45 cm in the period between May and June. These embryos were regarded as full term because they were easily separated from placenta implying that parturition would occur soon.

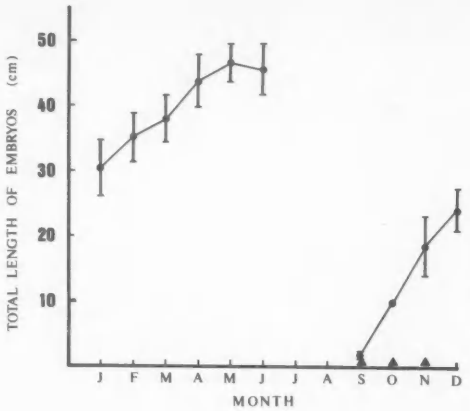

FIGURE 4.—Monthly growth of embryos of *Sphyrna lewini*. Solid triangles indicate the uterine eggs. Error represent 2 SD; numerals, sample size.

Counts of the number of uterine embryos as well as eggs of 110 gravid females (230–320 cm TL) ranged between 12 and 38 (mean 25.8). The relationship between the total number of uterine embryos or eggs and the size can be described by the regression equations (Fig. 5):

$$N = -26.105 + 0.179L,$$

where N is litter size, and L is total length in cm of the female. There is considerable variation in number of embryos with length, and the correlation coefficient r is low (0.567), but obviously fecundity is related to the size of the parent.

Examination of all females carrying developing embryos showed that occasionally some uterine eggs failed to develop. The number of nondeveloping uterine eggs carried by a single female was 1–4.

As with litter size, the number of ovarian eggs increased with the length of the adult female.

The embryos from 51 gravid females were sexed; of a total of 1,281 embryos, 637 were females. The sex ratios of embryos differed by litter; for instance, some individuals had predominantly male (13:5) or predominantly female (23:10) litters. But, as a whole, sex ratio was about 1:1.

The ratio of males to females for immature sharks in northeastern Taiwan waters was about 1:2 (42:91), but decreased to about 1:5 (95:446) for mature individuals (Table 1). There was no apparent increase in the relative number of males in the catch during the parturition season.

Discussion

Scalloped hammerhead sharks are abundant in the coastal seas around northeastern Taiwan, especially during the spring and winter, and are captured by harpoon or drift longlines at or near the surface. Rarely individuals smaller than 120 cm TL are captured because fishing gear and strategy are likely selective for larger fish. Clarke (1971) reported that in Hawaii, scalloped hammerhead pups usually stay close to the bottom.

Approximately equal numbers of male and female scalloped hammerhead sharks are born, although a much higher proportion of females than males are caught in the studied area. We are uncertain whether scalloped hammerhead females are more vulnerable to the fishing gear or are simply more numerous in this area. Similar predominances in females in the catch have been found in the scalloped hammerhead in the Gulf of California (Klimley 1981; Klimley and Nelson 1981). During the summer in 1979 off Baja California, females outnumbered males by 1.6× at Isla Cerrolvo, 3.8× at the El Bajo Seamount, and

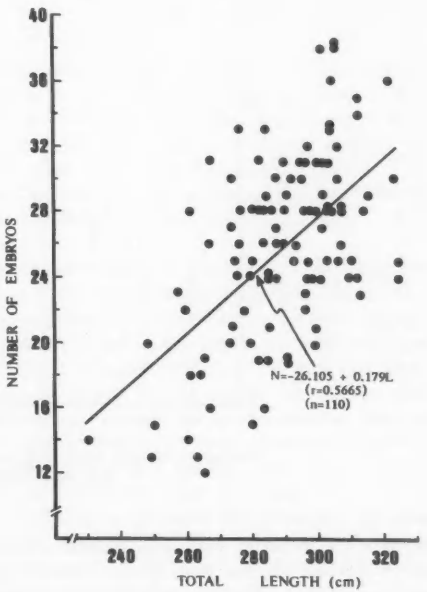

FIGURE 5.—Relationship between fecundity (number of uterine eggs or embryos) and total length of *Sphyrna lewini females*.

3.1× farther north at Isla Las Animas (Klimley 1981; Klimley and Nelson 1981). Similar disparities in sex ratios were also observed in sandbar sharks by Springer (1960). He felt that adult male sandbar sharks live over a large geographical and depth range, perhaps in deep cool oceanic waters inaccessible to the fishermen's gear, while females occur in warmer inshore water where they are more accessible to fishermen. He suggested that the males move inshore only to mate. We had insufficient data to test this suggestion in our sample area.

Castro (1983) reported that *S. lewini* from North American waters probably mature at about 180 cm; he did not mention whether this length referred to male, female, or both. Bass et al. (1975) reported that male scalloped hammerhead at Mozambique matured between 140 and 165 cm, reaching a maximum length of at least 295 cm; females matured at about 212 cm, reaching at least 309 cm. Compagno (1984) reported "maximum" sizes ranging from 370 to 420 cm. Our largest males were 305 cm TL, and the smallest mature male was 198 cm TL. The largest female observed was 324 cm, and the smallest mature female was 210 cm. It seems that in our sample area, males reached maturity at a somewhat larger size than in the other studied areas while females were about the same.

The close relationship of growth pattern of uterine embryos and ovarian eggs implies that eggs are transferred into the uterus and fertilized immediately after parturition. If the estimate of 10 month gestation period is correct, adult females give birth once each year.

The length at birth of scalloped hammerheads has been reported to be around 50 cm from Natal and southern Mozambique coastal waters (Bass et al. 1975), 43 cm from northeastern United States to Chesapeake Bay waters (Casey 1964), 38–45 cm in North American waters (Castro 1983), and 42–55 cm combined from all oceans (Compagno 1984). Our largest uterine embryos measured about 47 cm TL.

Pupping season appears to be during the summer in Taiwan as well as in Mozambique (Bass et al. 1975) and North America (Castro 1983). In Hawaii, Clarke (1971) found newborn pups throughout the year but with increased numbers in summer.

Acknowledgments

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Literature Cited

BASS, A. J., J. D. D'AUBREY, AND N. KISTNASAMY.
1975. Sharks of the east coast of southern Africa. III. The families Carcharinidae and Sphyrnidae. Oceanogr. Res. Inst., Durban, Invest. Rep. No. 38, 100 p.

CASEY, J. G.
1964. Angler's guide to sharks of the northeastern United States, Maine to Chesapeake Bay. Bur. Sport Fish. Wildl., Circ. No. 179, 32 p.

CASTRO, J. I.
1983. The sharks of North American waters. Texas A&M Univ. Press, 180 p.

CLARKE, T. A.
1971. The ecology of the scalloped hammerhead shark, *Sphyrna lewini*, in Hawaii. Pac. Sci. 25:133–144.

COMPAGNO, L. J. V.
1984. FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carchariniformes. FAO Fish. Synop. No. 125, 4(2):251–655.

KLIMLEY, A. P.
1981. Grouping behavior in the scalloped hammerhead. Oceans 24(4):65–71.

KLIMLEY, A. P. AND D. R. NELSON.
1981. Schooling of scalloped hammerhead shark, *Sphyrna lewini*, in the Gulf of California. Fish. Bull., U.S. 79:356–360.

SCHLERMITZAUER, D. A., AND P. W. GILBERT.
1966. Placentation and associated aspects of gestation in bonnethead shark, *Shyrna tiburo*. J. Morph. 120:219–231.

SPRINGER, S.
1960. Natural history of the sandbar shark, *Eulamia milberti*. U.S. Fish. Wildl. Serv., Bull. 61:1–38.

TESHIMA, K.
1981. Studies on the reproduction of Japanese smooth dogfish, *Mustelus manazo*, and *M. griseus*. J. Shimonoseki Univ. Fish. 29:113–119.

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OCCURRENCE OF YOUNG-OF-THE-YEAR KING, *SCOMBEROMORUS CAVALLA*, AND SPANISH, *S. MACULATUS*, MACKERELS IN COMMERCIAL-TYPE SHRIMP TRAWLS ALONG THE ATLANTIC COAST OF THE SOUTHEAST UNITED STATES[1]

King mackerel, *Scomberomorus cavalla*, and Spanish mackerel, *S. maculatus*, are migratory scombrids that support large recreational and commercial fisheries along the southeast coast of the United States (Manooch 1979). Recent evidence indicates that both species may be overexploited in portions of their range, prompting the South Atlantic Fishery Management Council to impose catch limits and landing quotas[2]. Many aspects of the biology and ecology of adult mackerels in this region have been studied (Manooch et al. 1978; Collette and Russo 1984), and the larval stages have also received attention (Fahay 1975; Collins and Stender 1987). However, little is known concerning the distribution and occurrence of juvenile (young-of-the-year) mackerels along the Atlantic coast of the southeastern United States, nor does it seem to be widely known that large numbers of these young fishes may be included in the bycatch of a major fishery. This report provides preliminary information on both of these topics.

Methods

During 1980–82 and 1985–86 the Marine Resources Monitoring and Assessment Program (MARMAP) at the South Carolina Marine Resources Research Institute conducted trawl surveys of the nearshore fish fauna in the South Atlantic Bight (Cape Hatteras, NC, to Cape Canaveral, FL). Before 1986, trawl gear consisted of two semiballoon shrimp trawls with an 18.3 m footrope, a 12.2 m headrope, 4.1 cm stretch mesh in the cod end, and 1.5 × 0.9 m doors towed at 2.5 knots (4.6 m/second). In 1986, paired "tongue" trawls with a 22.9 m footrope, 4.1 cm mesh, and 3.0 × 1.0 m doors were towed at approximately 2.5 knots. Sampling strategy and length of tow (20 minutes to 1 hour) varied between cruises. Station depths were 3–18 m in 1980–81 and 3–9 m in subsequent years. In each sample, all mackerels were identified to species and measured (fork length), and number and total weight were recorded for each species. We conducted two additional cruises in 1986 to test tongue trawl nets equipped with trawl efficiency devices (TED's). A National Marine Fisheries Service (NMFS) TED equipped with finfish deflector[3] was installed in one net, a Georgia TED[3] in a second net, and a third net acted as a control. The TED's were fished against each other and against the control for a total of 30 tows on the first cruise (July–August 1986) and 15 tows on the second (September–October 1986).

Tongue nets, also known as bib, falcon, cobra, or mongoose trawl nets, have become widely used by commercial shrimpers in some areas during recent years (Edwards 1987). The major difference between these and other common towed gears used in the penaeid shrimp fishery is a modified and elongated headrope that is held well above the footrope by attachment to the trawl warp with a third bridle. A large float, usually attached to the center of the headrope, produces a high, vertical mouth opening. The result is a net that fishes a larger portion of the water column than other common nets with similar footrope and door configurations.

Results

During years when semiballoon nets were used, catch per unit effort of mackerels was relatively low (king mackerel: 0.2–0.4 individuals/net-hour; Spanish mackerel: 0.3–2.2 individuals/net-hour). Tongue trawl nets on four 1986 cruises gave cruise-specific average catches of 2.5–8.7 individuals/net-hour for king mackerel and 12.4–115.2 individuals/net-hour for Spanish mackerel, using catches of control [unmodified] nets for TED cruises (Table 1). Both species were taken as late as 30 October, except for two king mackerel caught in December 1982. Approximately 79% of king and 91% of Spanish mackerel were caught in depths <9 m during the two years in which sample depths extended to 18 m.

Mackerels taken in shrimp trawls were almost entirely juvenile fishes. Rather than pool catches between cruises that often differed in time of year, geographic area, and sampling strategy, examples of length frequencies of Spanish and king

[1]Contribution No. 244 of the South Carolina Marine Resources Center.

[2]South Atlantic Fishery Management Council, Council Meeting Summary, 27-29 April 1987, Charleston, SC.

[3]Described and illustrated in the Federal Register, vol. 52, no. 124; Monday, June 29, 1987 - Rules and Regulations; p. 24244–24262.

TABLE 1.—Results of nearshore cruises using two types of shrimp trawls.

Cruise dates	Net type	Sampling[1] strategy	Sample area[2]	Total net-hour	No. Spanish	No. kings
July–Sept. 1980	semiballoon	SR+NR	NC, SC, GA, FL	114	250	40
Apr.–June 1981	semiballoon	SR	NC, SC, GA, FL	77	21	13
Sept. 1982–Jan. 1983	semiballoon	SR	NC, SC, GA, FL	73	27	27
Aug.–Sept. 1985	semiballoon	SR+NR	NC, SC, GA, FL	59	120	36
Aug.–Sept. 1986	tongue	NR	NC, SC, GA, FL	41	1,421	104
Oct. 1986	tongue	SR	NC, SC, GA	55	681	481
July–Aug. 1986	tongue	NR	SC	20	2,303	84
Sept.–Oct. 1986	tongue	NR	SC	20	327	80

[1]SR = stratified random sampling; NR = nonrandom sampling.
[2]At least some portions of the waters of these states were sampled.

mackerels taken in tongue nets on two cruises are presented in Figures 1 and 2, respectively. Comparisons of the catch rates of Spanish mackerel during the TED evaluations in July–August 1986 showed that significantly fewer were taken in the tongue net equipped with a NMFS TED than the control net (Mann-Whitney: $P < 0.001$) or the Georgia TED-net ($P < 0.05$) (Table 2). There were no significant differences in catches of king mackerel (Table 3), or in catches of either species between nets on the September–October cruise, perhaps due to the smaller sample sizes.

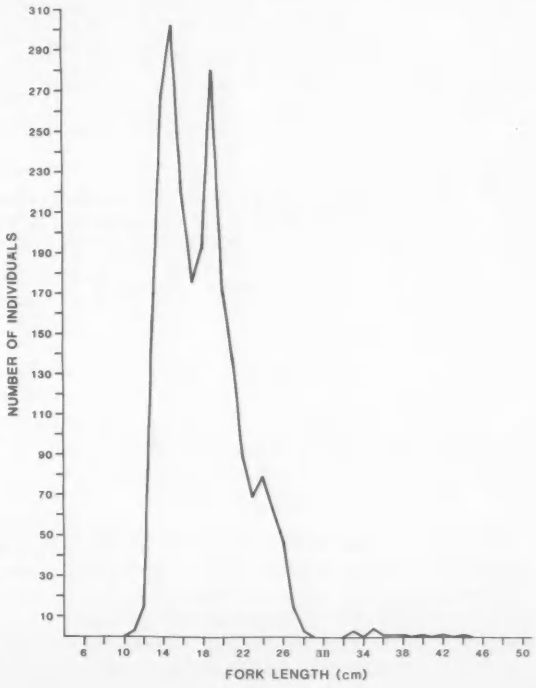

FIGURE 1.—Length-frequency distribution of Spanish mackerel taken in shrimp tongue trawl nets during July–August 1986 along the southern Atlantic coast of the United States (n = 2,303).

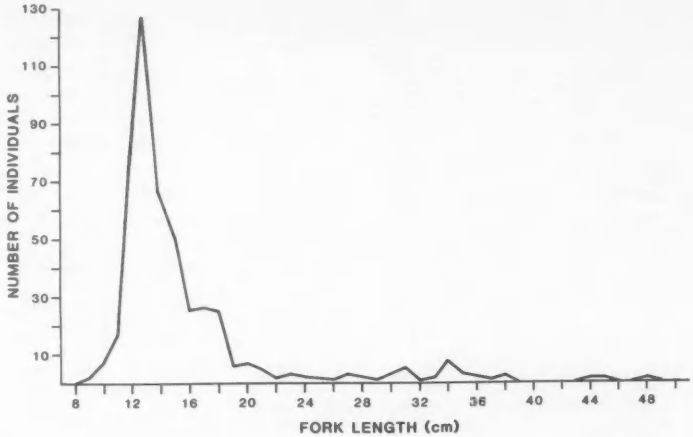

FIGURE 2.—Length-frequency distribution of king mackerel taken in shrimp tongue trawl nets during October 1986 along the southern Atlantic coast of the United States (n = 481).

TABLE 2.—Catches of Spanish mackerel during evaluations of tongue nets equipped with trawl efficiency devices (TED's). C = 22.9 m footrope length tongue net; NMFS = 22.9 m footrope length tongue net with a NMFS TED; GA = 22.9 m footrope length tongue net with a Georgia TED. Tow times = 1 hour.

Cruise	Comparison	No. of tows	Net type	No. of Spanish mackerel			Net type	No. of Spanish mackerel		
				Total	$\bar{x} \pm$ SD	Range		Total	$\bar{x} \pm$ SD	Range
July–Aug.	C-NMFS	10	C	1,104	110 ± 27	68–144	NMFS	519	52 ± 23	12–73
	C-GA	10	C	1,199	120 ± 65	40–276	GA	1,219	122 ± 74	44–300
	NMFS-GA	10	NMFS	880	88 ± 53	35–176	GA	1,650	165 ± 142	67–533
Sept.–Oct.	C-NMFS	5	C	104	21 ± 15	2–41	NMFS	53	11 ± 11	2–27
	C-GA	5	C	206	41 ± 38	1–103	GA	155	31 ± 28	0–76
	NMFS-GA	5	NMFS	108	22 ± 23	4–58	GA	149	30 ± 25	3–59

TABLE 3.—Catches of king mackerel during evaluations of tongue nets equipped with trawl efficiency devices (TED's). C = 22.9 m footrope length tongue net; NMFS = 22.9 m footrope length tongue net with a NMFS TED; GA = 22.9 m footrope length tongue net with a Georgia TED. Tow times = 1 hour.

Cruise	Comparison	No. of tows	Net type	No. of king mackerel			Net type	No. of king mackerel		
				Total	$\bar{x} \pm$ SD	Range		Total	$\bar{x} \pm$ SD	Range
July–Aug.	C-NMFS	10	C	41	4 ± 4	1–13	NMFS	46	5 ± 9	0–30
	C-GA	10	C	43	4 ± 5	0–15	GA	41	4 ± 4	0–13
	NMFS-GA	10	NMFS	23	2 ± 3	0–8	GA	26	3 ± 5	0–17
Sept.–Oct.	C-NMFS	5	C	26	5 ± 7	0–15	NMFS	14	3 ± 3	0–5
	C-GA	5	C	40	8 ± 8	4–22	GA	22	4 ± 5	1–14
	NMFS-GA	5	NMFS	24	5 ± 2	2–8	GA	20	4 ± 4	2–11

Discussion

Although it is possible that juvenile mackerels were more abundant in 1986 than in previous years, the increased catches of these fishes in tongue nets over semiballoon nets suggests that the former are much more efficient in capturing these fishes. Preliminary data from a gear comparison cruise in 1987 indicate that tongue nets do catch more pelagic fishes than semiballoon nets even after adjusting for differences in footrope lengths (G. Sedberry[4]). Unfortunately,

[4]G. Sedberry, Marine Resources Research Institute, South Carolina Wildlife and Marine Resources Department, P.O. Box

these tests were conducted during March–April when juvenile mackerels are rare in the coastal waters of South Carolina.

In 1986 we collected juvenile mackerels during July through October. Because of incomplete temporal sampling, we do not know if they were present earlier and later in the year in this region. Based on the occurrence of early larval stages, spawning of both mackerels in the South Atlantic Bight extends from May through at least September (Collins and Stender 1987). If growth rate estimates of ca. 3 mm/day for juveniles are correct (M. R. Collins, unpubl. data), king mackerel spawned in early May could be recruited into the bycatch of the shrimp fishery in June. Late-spawned fish from the previous year may also be present at this time. In South Carolina, the open season for commercial trawling for penaeid shrimps in state waters usually extends from June through December, which coincides with the presence of juvenile mackerels in the heavily fished nearshore waters. In addition, mackerels were much more abundant in tows made in depths <9 m, which includes the preferred shrimping areas, than in deeper waters. This may be due either to greater abundance in these depths or to greater catchability in response to the fact that the trawl nets fish a larger portion of the water column in shallower areas.

It is difficult to accurately estimate the bycatch of mackerels in the commercial shrimp fishery owing to lack of current, detailed information from throughout the region on number of vessels, effort expended, gears used, and areas fished. However, our catch rates suggest that the impact of tongue nets on mackerel stocks may be significant. As the current status of these stocks is such that strong restrictions have been imposed on both the recreational and commercial fisheries, it is unfortunate that the situation may be exacerbated by a potentially large bycatch of juvenile mackerels in the shrimp fishery. More information is needed on the ecology and behavior of young mackerels, and their vulnerability to various gears, in order to resolve this conflict.

Acknowledgments

We wish to express our appreciation to the many people who assisted in the tedious tasks of collecting and processing trawl samples over the years, including the captains and crews of the vessels involved. This work was sponsored by the National Marine Fisheries Service (Southeast Fisheries Center), the South Carolina Wildlife & Marine Resources Department, and the Sport Fishery Research Foundation.

Literature Cited

COLLETTE, B. B., AND J. L. RUSSO.
1984. Morphology, systematics, and biology of the Spanish mackerels (*Scomberomorus*, Scombridae). Fish. Bull., U.S. 82:545–692.

COLLINS, M. R., AND B. W. STENDER.
1987. Larval king mackerel (*Scomberomorus cavalla*), Spanish mackerel (*S. maculatus*), and bluefish (*Pomatomus saltatrix*) off the southeast coast of the United States, 1973–1980. Bull. Mar. Sci. 41:822–834.

EDWARDS, M. L.
1987. The shrimp trawl. Natl. Fisherman 67(13):89–92.

FAHAY, M. P.
1975. An annotated list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV *Dolphin* cruises between May 1967 and February 1968. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-685, 39 p.

MANOOCH, C. S., III.
1979. Recreational and commercial fisheries for king mackerel, *Scomberomorus cavalla*, in the South Atlantic Bight and Gulf of Mexico, U.S.A. *In* E. L. Nakamura and H. R. Bullis (editor), Proceedings of the mackerel colloquium, p. 33–41. Gulf States Mar. Fish. Comm., Brownsville, TX.

MANOOCH, C. S., III, E. L. NAKAMURA, AND A. B. HALL.
1978. Annotated bibliography of four Atlantic scombrids: *Scomberomorus brasiliensis*, *S. cavalla*, *S. maculatus*, and *S. regalis*. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 418, 166 p.

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STOMACH CONTENTS OF COMMERCIALLY CAUGHT HUDSON RIVER STRIPED BASS, *MORONE SAXATILIS*, 1973–75

The Hudson River estuary is a detritus-driven ecosystem. Only a few of the 100 or more reported fish species function as tertiary piscivores more typical of a grazing food chain. Of these few species, which include the American eel, *Anguilla rostrata*, and the summer-transient juvenile

12559, Charleston, SC 29412, pers. commun. May 1987.

bluefish, *Pomatomus saltatrix*, striped bass, *Morone saxatilis*, are probably the most important in terms of biomass and commercial value. However, commercial fishing for the American eel and striped bass has been banned in the Hudson since 1976 because both species are contaminated with higher levels of toxic polychlorinated biphenyls (PCB's) than most other Hudson River fish species.

To date, only one published paper has touched upon the diet of prespawning Hudson River striped bass larger than 400 mm TL (Gardinier and Hoff 1982), and their results for fish of that size are based on less than 10 samples for which fish remains were identified to species or family level. The present paper describes the findings of stomach content analysis for 510 striped bass, most of which were prespawning adults larger than 400 mm TL (Fig. 1) collected during the spring months of 1973–75 by commercial gill nets in the Tappan Zee region of the Hudson River.

Description of Sampling Area and Methods

The Tappan Zee gill-net fishery is located approximately 90 m south of the Tappan Zee Bridge at river km 43.5 (measured from the Manhattan Battery) in a relatively shallow section that is 4.5 km wide, a location through which many of the spawners move on the way to upstream spawning grounds. The staked gill nets were set perpendicularly to the north-south current in water depths of 2.4–9.8 m and spanned a distance of approximately 1.6 km out to the dredged channel on the east side of the river. Stretched mesh sizes were 11.4, 11.8, 12.1, 12.7, 13.3, and 14.0 cm. Water temperatures during the sampling period ranged from approximately 6° to 19.5°C, and the salinity was essentially that of freshwater, rarely rising above 300 mg/liter. Sampling dates included the following periods in each year: 28 March–9 May 1973, 8 April–20 May 1974, and 6 April–19 May 1975. Fish were collected from the nets at 8–12 h intervals, placed on ice, and taken directly to a laboratory for total length (TL) measurements and stomach content analysis. Prey items were identified with the aid of a binocular dissecting scope and frequency of occurrence was noted.

Results

Stomach Content Analysis

A summary table of stomach content data, pooled for the three years of analysis (Table 1), shows that adult, prespawning striped bass were highly piscivorous and that 89% of the stomachs containing identified food items contained fish and 21% contained invertebrate remains, primarily those of *Crangon* species. Clupeid species were the most prevalent fish, with blueback herring, *Alosa aestivalis*, predominating. Most of the clupeids were adult, prespawning herring, approximately 200 mm TL.

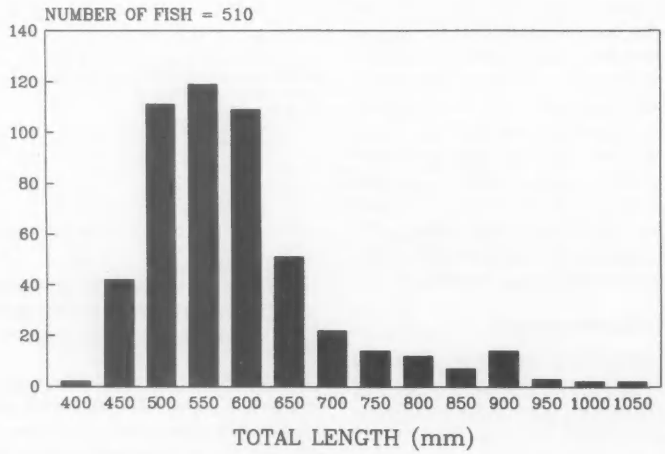

FIGURE 1.—Length distribution of Hudson River striped bass examined for stomach contents.

TABLE 1.—Stomach contents of adult prespawning striped bass collected by commercial gill net during spring 1973, 1974, and 1975.

Food item	Number of stomachs in which item occurred	% Frequency of occurrence based on total stomachs analyzed (n = 510)	% Frequency of occurrence based on number of stomachs containing identified food items (n = 201)
Fish	179	35.1	89.1
Clupeidae	73	14.3	36.3
Alosa pseudoharengus	13	2.5	6.5
Alosa aestivalis	29	5.7	14.4
Brevoortia tyrannus	3	0.6	1.5
Clupeidae	28	5.5	13.9
Morone spp.	9	1.8	4.5
Morone americana	6	1.2	3.0
Morone saxatilis[1]	1	0.2	0.5
Morone spp.	2	0.4	1.0
Other fish	29	5.7	14.4
Ammodytes americanus	14	2.7	7.0
Microgadus tomcod	7	1.4	3.5
Osmerus mordax	2	0.4	1.0
Syngnathus fuscus	2	0.4	1.0
Anchoa mitchilli	2	0.4	1.0
Ictalurus catus	1	0.2	0.5
Scomber scombrus	1	0.2	0.5
Unidentified fish remains	68	13.3	33.8
Invertebrates	43	8.4	21.4
Crangon spp.	38	7.5	18.9
Polychaeta	5	1.0	2.5
Unidentified contents	11	2.2	Not applicable
Total stomachs analyzed			510
Number (percent) containing identified food items			201 (39.4)
Number (percent) containing food material (identified and unidentified)			212 (41.6)
Number (percent) empty			296 (58.4)

[1]Two yearling striped bass in female collected 15 April 1974.

The next most abundant fish prey species in the composite 1973–75 sample was the American sand lance, *Ammodytes americanus*. Sand lance were present in striped bass stomachs only during 1975, when the frequency of occurrence was about 11% (Fig. 2). Atlantic tomcod, *Microgadus tomcod*, were found in striped bass stomachs only during 1973 when the frequency of occurrence was about 20%, somewhat higher than the frequency of clupeid species for that year (Fig. 2). These fish were yearling, postspawning Atlantic tomcod averaging about 125 mm TL. The *Morone* species, white perch, *M. americana*, and striped bass, had a frequency of occurrence of 4.5% for the composite sample and were present in striped bass stomachs every year (Fig. 2).

Discussion

Similar to findings in this study, Trent and Hassler (1966) found that blueback herring were predominant in the diet of adult, prespawning striped bass from the Roanoke River, NC, and Manooch (1973) found that herring ranked second after Atlantic menhaden, *Brevoortia tyrannus*, in the spring diet of adult striped bass from Albemarle Sound, NC. Data from Gardinier and Hoff (1982) do not indicate that blueback herring or clupeids were important in the diet of prespawning Hudson River striped bass collected during 1976 and 1977, but fish remains in bass stomachs were generally not identified to the family or species level in their study.

American sand lance are rarely found over muddy bottoms (Bigelow and Schroeder 1953; Leim and Scott 1966) or within estuaries (Massman 1960; Norcross et al. 1961), but they ranked second only to blueback herring in the diet of Hudson River striped bass. Sand lance were not reported from the Hudson River prior to 1975 when adults and larvae were relatively abundant in February–April ichthyoplankton collections south of the Tappan Zee Bridge (Dew and Hecht 1976). Data from the present study (Fig. 2) and from early spring ichthyoplankton sampling during 1976 (Dew, unpub. data), indicate that sand lance are not abundant every year in the Hudson, but it is probable that during some years adult sand lance serve as important alternate prey for prespawning striped bass.

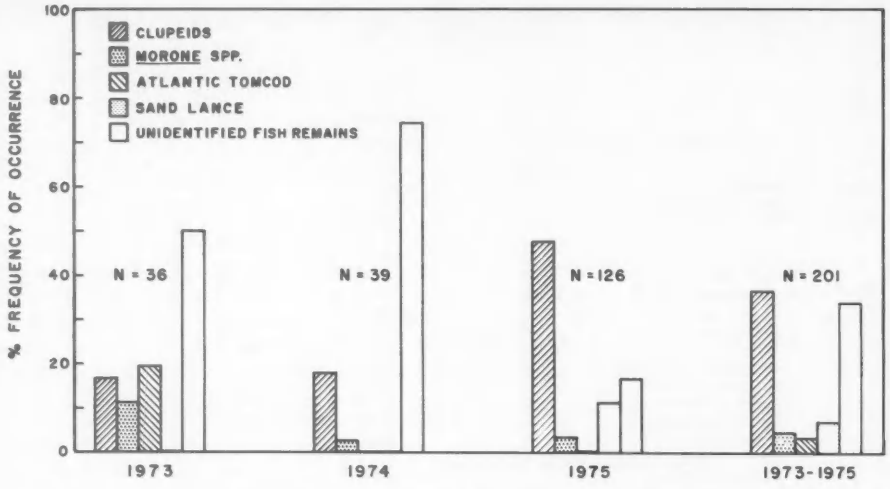

FIGURE 2.—Percent frequency of occurrence of fish prey categories based on number of stomachs containing identified food.

The fact that Atlantic tomcod were found only during 1973 may be due to a sampling artifact because 1973 was the only year in which March samples were taken, and all tomcod prey were found during March 1973. In March, gravid alewives, *Alosa pseudoharengus*, and blueback herring have not yet moved into the estuary and, prior to the arrival of these apparently preferred prey species, Atlantic tomcod may serve as an alternate forage fish. Thus the winter-spawning Atlantic tomcod may be a regular diet item at a time when alternate prey species are not available.

It is evident from Table 1 that there are several alternate fish prey for striped bass in the Hudson River (e.g., blueback herring, sand lance, alewife, Atlantic tomcod, white perch, and striped bass), and it is expected that striped bass predation upon these species would be of a compensatory nature. In a simple predator-prey situation where there are no alternate prey, predation is often depensatory (Neave 1953) because a population of predators would tend to seek out and consume a high proportion of small year classes and a lower proportion of strong year classes. In a more complex community where there are several species of prey, predation may be compensatory if predators change their feeding habits in response to the availability of food (Ivlev 1961; Forney 1971). That is, if several equally suitable prey species were available within a system, the predator species would tend to feed more heavily on the most abundant species, thus acting in a compensatory manner.

The ratio of white perch to striped bass in stomach samples identified to the species level is 6:1 (Table 1). This ratio is based on a small sample size, but it closely approximates the long-term average ratio of 5.9:1 for annual CPUE values for white perch and striped bass collected in several hundred bottom trawls from the Haverstraw Bay region (Milepoint 36) during 1971–77 (Lawler, Matusky and Skelly Engineers unpubl. data). In other words, yearling and older white perch and yearling striped bass may be equally attractive prey species, and their frequency of occurrence in adult striped bass stomachs may depend primarily upon the frequency of random encounters rather than active prey selection. If this were true, the frequency of cannibalism should be greatest during those years when the abundance of yearling striped bass relative to white perch (and other species) was greatest.

Acknowledgments

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Literature Cited

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. Fish. Bull. 53:1–577.

DEW, C. B., AND J. H. HECHT.
1976. Observations on the population dynamics of Atlantic tomcod *Microgadus tomcod* in the Hudson River estuary. Proc. Fourth Symposium On Hudson River Ecology, Paper 25. Hudson River Environmental Society, Bronx, N.Y.

FORNEY, J. L.
1971. Development of dominant year classes in a yellow perch population. Trans. Am. Fish. Soc. 100:739–749.

GARDINIER, M. N., AND T. B. HOFF.
1982. Diet of striped bass in the Hudson River estuary. New York Fish Game J. 29(2):152–165.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, 302 p.

LEIM, A. H., AND W. B. SCOTT.
1966. Fishes of the Atlantic coast of Canada. Fish. Res. Board Can. Bull. 155, 485 p.

MANOOCH, C. S.
1973. Food habits of yearling and adult striped bass, *Morone saxatilis* (Walbaum), from Albemarle Sound, North Carolina. Chesapeake Sci. 14(2):73–86.

MASSMANN, W. H.
1960. Additional records for new fishes in Chesapeake Bay. Copeia 1960:1–70.

NEAVE, F.
1953. Principles affecting the size of pink and chum salmon populations in British Columbia. J. Fish. Res. Board Can. 9:450–491.

NORCROSS, J. J., W. H. MASSMANN, AND E. B. JOSEPH.
1961. Investigations of inner continental shelf waters off lower Chesapeake Bay. Part II. Sand lance larvae, *Ammodytes americanus*. Chesapeake Sci. 2(1–2):49–59.

TRENT, L., AND W. W. HASSLER.
1966. Feeding behavior of adult striped bass, *Roccus saxatilis*, in relation to stages of sexual maturity. Chesapeake Sci. 7(4):189–192.

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ACCUMULATION OF AGE PIGMENTS (LIPOFUSCIN) IN TWO COLD-WATER FISHES

In fisheries management, age structured models are the preferred method for meeting the key objectives of estimating optimal yields and determining the effect of fishing on stock structure (Gulland 1978). However, few species of commercial marine fishes exist in which age can be determined with certainty (Boehlert 1985). The concentration of age pigments (lipofuscin) (Ettershank 1984) in fish tissues (Agius and Agbede 1984) may be a measure of fish age that could be used to validate other ageing techniques and might also improve estimates of age of long-lived species where other techniques are difficult to apply.

Lipofuscin originates in biological membranes through lipid peroxidation (Tappel 1975). Lipofuscin accumulation has been documented for a wide variety of animals, from mammals to the bread-mold *Neurospora* (Ettershank et al. 1983 and references therein). The rate of accumulation has been shown to be constant during the lifetime of laboratory-raised mice (Reichel 1968; Miquel et al. 1978), dogs (Munnell and Getty 1968), fleshflies (Ettershank et al. 1983); man (Strehler et al. 1959); and also wild populations of mice (Dapson et al. 1980). On the other hand, the rate of lipofuscin accumulation has been shown to vary with level of activity and lifespan (Sohal and Donato 1978). It is expected that the rate in which lipofuscin accumulates with age in a natural population of fishes, or stock, with its free genetic interchange and likely common habitat, would be fairly uniform (but see Smith 1987). In addition, if measurements are made in nonmitotic and constantly metabolizing tissues such as brain or myocardium, the variation in concentration due to environmental effects is least likely.

In this paper we present the results of a preliminary study designed to assess the usefulness of extracted lipofuscin as a method of ageing fishes. Two species of cold-water fishes are included: the rainbow trout, *Salmo gairdneri*, reared in captivity, and of known age; and the Dover sole, *Microstomus pacificus*, a long-lived fish, in which age is not known with certainty. We present spectral characteristics of the extracted lipofuscin from several tissues and the change in concentration of lipofuscin with fish age.

Materials and Methods

Specimens of Dover sole were collected on December 1986 off Point Conception. Ages were estimated by J. Butler, E. Lynn, and M. Drawbridge of the Southwest Fisheries Center using otolith sections. Ages ranged from 2.7 to 44.7 years (average of three readings). Specimens of the species *Salmo gairdneri* were collected in July 1986 at Hot Creek Hatchery. Ages ranged from 3 months to 3 years.

Samples were frozen after collection and kept at −80°C until analysis. Studies by Nicol (1987) showed that this form of preservation yielded the lowest fluorescence when compared with ethanol and formalin-preserved samples. There was no indication that the level of fluorescence changed as a function of time of preservation or by interaction with the extracted lipofuscin, as in the case for formalin. To excise the brain, the top of the skull was opened and the four brain lobes were removed as a unit, without the optic nerve. To excise the heart, we separated the muscle from connective tissue, blood vessels, and fat deposits.

Three methods were compared for maximum lipofuscin extraction. The first two methods (Tappel 1975; MacArthur and Sohal 1982) were specifically developed for lipofuscin extraction and employed chloroform:methanol (2:1) as the extractive solvent; they differ in the optimal volume-to-weight ratio (30:1 and 20:1, respectively), temperature of extraction, and number of times the chloroform phase is washed with water. The third method was developed for lipid extraction in fishes (Bligh and Dyer 1959) and uses chloroform:methanol:water (1:2:0.8) as the extractive solvent. Subsamples ($n = 3$) of cerebellum of *Stenella* sp. collected at the eastern tropical Pacific and kept at −30°C were defrosted, dried with lint-free paper, weighed, and extracted following the three methods as described originally.

Tissues from Dover sole were extracted basically following the MacArthur and Sohal (1982) technique, with two additional steps to ensure a complete washing out of flavoproteins and photooxidation of retinol when present (Fletcher et al. 1973). Tissue was freeze dried prior to analysis. Ten mL of chloroform:methanol (2:1, v/v) was added to a homogenizer containing the sample for a final solvent:sample ratio of about 120:1 (vol/dry weight). The sample was ground with a teflon pestle attached to an electric drill and later submerged in a 40°C water bath for 1 minute. A 2 mL subsample was taken from the homogenate. Three mL of deionized water was added, the sample was shaken, and the emulsion centrifuged 10 minutes at 1,912 *g* and 0°C. After centrifugation, the hyperphase was decanted and a second rinse performed. After decanting the hyperphase a second time, 1 mL of the hypophase (chloroform containing lipofuscin) was sampled and transferred to a polypropylene tube. Three mL of chloroform were added to the sample (for a total of 4 mL) which was then exposed to UV irradiation (254 nm) for 1–2 minutes to photooxidize retinol. This last step was routinely performed for liver tissue.

Samples were then transferred to glass tubes, sealed, and kept in the refrigerator until analysis. Sample fluorescence was measured at the emission peak (430–440 nm) in a quartz cuvette with a Perkin Elmer Fluorescence Spectrophotometer[1] Model MFP-44A. The sample was excited at the peak of fluorescence excitation (~360 nm). The intensity of the fluorescent emission (at 430 nm) was normalized to the intensity of the quinine solution standard (1 mg L^{-1} in 1N sulphuric acid) and expressed in fluorescence units.

Lipofuscin in Dover sole is expressed as 1) total lipofuscin content per organ and 2) weight-specific lipofuscin concentration, calculated by dividing the total lipofuscin content by the dry weight of the entire organ.

Lipofuscin from rainbow trout tissues was extracted following the Bligh and Dyer (1959) technique, without modifications. Whole tissues were ground in water with a tissue homogenizer to give a final concentration of 100 mg of tissue (wet weight) in 0.8 mL of homogenate. A sample of 0.8 mL was taken and solvents were added to give a final ratio of 1:2:0.8 (chloroform:methanol:water) with a solvent to sample ratio of 20:1 (vol/w). The sample was then filtered through a 2.4 cm glass fiber filter (Whatman GF/C), the tissue re-extracted with 1 mL of chloroform and refiltered. The extract was then washed with 3 mL of water, shaken, and centrifuged for 10 minutes at 1,912 *g* and 0°C. One mL of the chloroform hypophase was subsampled and fluorescence estimated as described above.

Lipofuscin in rainbow trout is expressed as 1) total lipofuscin content per organ and 2) weight-specific lipofuscin concentration (total lipofuscin content of the organ divided by its wet weight).

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

Efficiency of Extraction

Lipofuscin was successfully extracted and quantified from three different fish tissues: brain, heart, and liver. Wavelengths of fluorescence excitation and emission maxima of extracted lipofuscin in chloroform are presented in Figure 1. All maxima are within the range cited by Sheldahl and Tappel (1973); fluorescence excitation maxima were between 340 and 370 nm and fluorescence emission maxima between 420 and 470 nm.

Retinol (wavelengths of maximum fluorescence excitation at 325–340 nm and maximum fluorescence emission at 475 nm) was photooxidized by exposing the chloroform extract to UV irradiation (254 nm). As expected, retinol was found in liver and sometimes it was present in brain and heart tissues. For example, wavelengths of fluorescence excitation and emission maxima in liver of Dover sole shifted from 352 to 365 nm and from 470 to 440 nm, respectively, after UV irradiation (see Figure 1C). Mullin and Brooks (1988) also found that this UV irradiation is effective in oxidizing retinol although they did not find significant retinol interference in fish tissue. It seems liver tissues may require UV irradiation to oxidize retinol while brain and heart tissue should be checked for retinol presence before irradiation.

The extractive efficiency of the three methods tested are compared in Table 1. All methods extracted similar fluorescent compounds from the brain of *Stenella* sp., as the fluorescence excitation and emission spectra were similar. The MacArthur and Sohal (1982) method extracted significantly more fluorescent pigment, than did either the Tappel (1975) or the Bligh and Dyer (1959) method which extracted 66% and 46% of maximum extraction, respectively). Thus all three methods are useful for quantitative estimation of extractable lipofuscin in fish tissue but

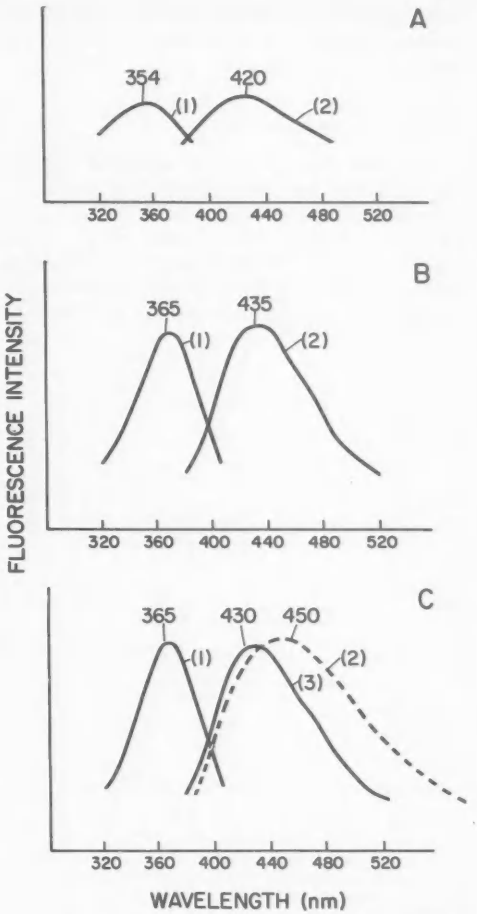

FIGURE 1.—Spectral characteristics of lipofuscin extracted from Dover sole, *Microstomus pacificus*, tissues (uncorrected spectra). In chloroform. (A) Brain: (1) Lipofuscin fluorescence excitation spectrum (emission wavelength 440 nm); (2) lipofuscin fluorescence emission spectrum (excitation wavelength 365 nm). (B) Heart: (1) Lipofuscin excitation spectrum (emission wavelength 430 nm); (2) lipofuscin fluorescence emission spectrum (excitation wavelength 365 nm). (C) Liver: (1) Lipofuscin fluorescence excitation spectrum (emission wavelength 430 nm); (2) lipofuscin emission spectrum (excitation wavelength 365 nm) before UV radiation; (3) Same as (2) after UV radiation (254 nm).

TABLE 1.—Comparison of the three methods of lipofuscin extraction in brain tissue. Fluorescence excitation at 360 nm and fluorescence emission at 440 nm. Results are presented as fluorescence units per mg of wet tissue, where the fluorescence emission signal is normalized to the intensity of emission of a standard quinine sulfate solution (1 mg L^{-1} in 1N sulphuric acid). The three methods were significantly different from each other, $P < 0.05$, Newman-Keuls range test (Zar 1974). ANOVA: F ratio = 21.81, 2 df, $P < 0.05$.

	Fluorescence units			Fluorescence maxima	
	Average 10–3	SD 10–3	*n*	Excitation (nm)	Emission (nm)
MacArthur and Sohal (1982)	4.30	0.39	3	362	445
Tappel (1975)	2.83	0.37	3	362	440
Bligh and Dyer (1959)	1.98	0.45	3	360	445

comparisons of amount of concentrations between tissues or species cannot be made if different extraction methods are used.

Lipofuscin Concentration

The total concentration of extracted lipofuscin in Dover sole brain tissue was positively correlated with fish length (Fig. 2A) ($Y = -15.4 + 0.516\,X$, $r^2 = 0.43$; $b \neq 0$, $P < 0.01$, $t = 5.1$, df = 34). Furthermore, total extracted lipofuscin content in the brain was positively correlated with age in organisms estimated by annular increments in otoliths to be from 2 to 15 years old (Fig. 3A) ($Y = -2.5 + 1.0\,X$, $r^2 = 0.75$; $b \neq 0$, $P < 0.01$, $t = 5.5$, df = 10). On the other hand, in older Dover sole (estimated age from 20 to 45 years; $n = 26$) the total extracted lipofuscin in the brain did not increase with their estimated age. The concentration of lipofuscin in the brain (extracted lipofuscin concentration per unit of g dry weight) followed a similar pattern (Fig. 3B). The concentration in the brain increased linearly with age for fish 2–15 years old ($Y = 30.39 + 14.85\,X$, $r^2 = 0.79$, $b \neq 0$, $P < 0.01$, $t = 6.66$, df = 10) but fishes older than 15 years did not show an increase in pigment concentration with age.

The total extracted lipofuscin content extracted from rainbow trout brains increased with age (Fig. 4A) ($Y = 0.14 + 0.18\,X$, $r^2 = 0.37$; $b \neq 0$, $P < 0.01$, $t = 3.75$, df = 23), as did the content of the heart (Fig. 4C) ($Y = -0.54 + 0.82\,X$, $r^2 = 0.67$; $b \neq 0$, $P < 0.01$, $t = 7.36$, df = 23), and liver (Fig. 4E) ($Y = -2.86 + 5.81\,X$, $r^2 = 0.62$; $b \neq 0$, $P < 0.01$, $t = 7.54$, df = 34) from 3 months to 3 years. The concentration of extracted lipofuscin per unit wet weight of heart tissue did not change with age (Fig. 4D) whereas that of brain and liver tissue decreased with age (Fig. 4B, F).

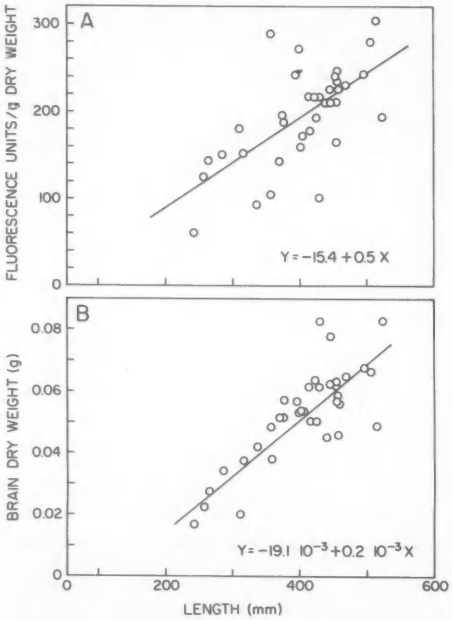

FIGURE 2.—Dover sole, *Microstomus pacificus*, brain: (A) Extracted lipofuscin per unit of dry weight as a function of fish length (mm) (n = 36); (B) brain dry weight (g) as a function of fish length (mm). Fluorescence units: the intensity of fluorescence normalized to a standard solution of quinine sulfate (1 mg L^{-1} in 1N sulphuric acid).

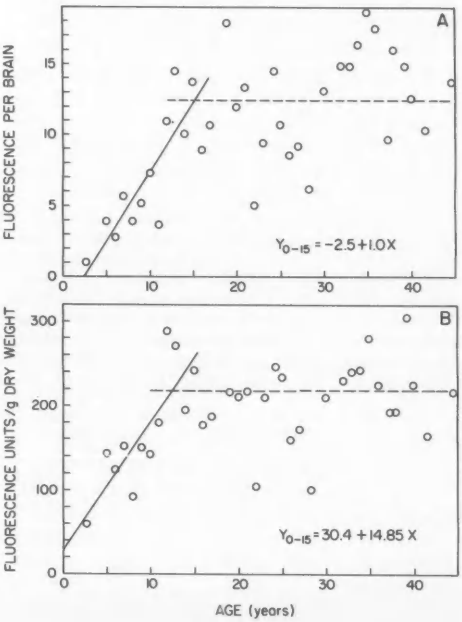

FIGURE 3.—Lipofuscin in Dover sole, *Microstomus pacificus*, brain tissue as a function of age ($n = 36$). (A) Total lipofuscin content per brain; (B) weight-specific (g dry weight) lipofuscin in brain.

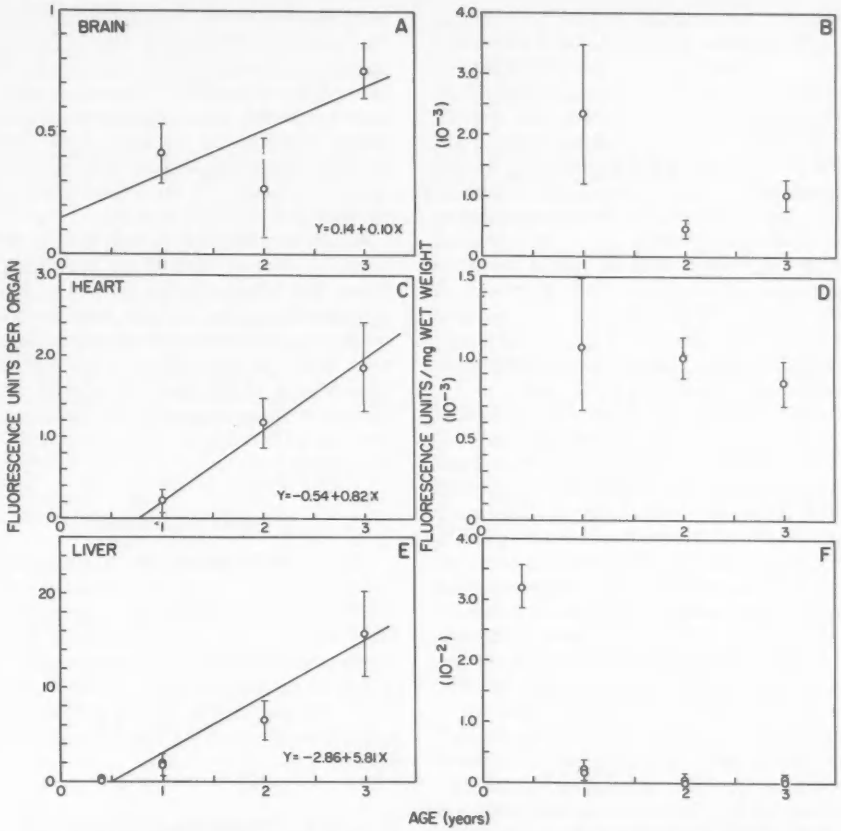

FIGURE 4.—Lipofuscin in rainbow trout, *Salmo gairdneri*, as a function of age (n = 21). (A) Total lipofuscin in brain; (B) weight-specific (mg wet weight) lipofuscin in brain; (C) total lipofuscin in heart; (D) weight-specific (mg wet weight) lipofuscin in heart; (E) total lipofuscin in liver; (F) weight-specific (mg wet weight) lipofuscin in liver.

Discussion

Our results indicate that lipofuscin accumulated in the brain of Dover sole with time (Fig. 2A). The concentration of lipofuscin increased over a wide range of fish lengths and with estimated age of 15 years but did not increase with older fish. Several explanations exist for the lack of change in concentration in older fish: 1) older fish were incorrectly aged; 2) growth of brain tissue masked the actual rate of accumulation; and 3) the rate of accumulation changed during the lifespan of this species due to changes in metabolic activity. Either one or several of these factors may cause the lack of lipofuscin accumulation in older fish. We consider each of these issues below.

We do not know the accuracy of the age determination in Dover sole but believe it is unlikely that 3 readers would confuse fish aged 30–40 years with those of 20 years. Although future research will shed more light on this controversial subject, we think that grossly inaccurate age determination is the least likely an explanation.

A key difference between fishes and other organisms in which lipofuscin accumulation has been clearly documented as a function of chronological age (mammals and invertebrates) is that

fishes have indeterminate growth. For example, Figure 3B indicates that the brain of Dover sole continues to grow long after this fish begins reproduction (450 mm). Thus, unlike mammals and invertebrates which have determinate growth, the total content of extractable lipofuscin in any fish organ cannot be used as a measure of age but rather concentration (content per unit of weight) must be used. Furthermore, even the concentration of lipofuscin in the brain, a slow growing tissue, is a function of both the rate of lipofuscin accumulation and the rate of tissue growth. It follows then, that if the rate of brain growth is such that it masks the actual rate of lipofuscin accumulation in older organisms, lipofuscin concentration will not increase with time.

A critical assumption underlying the use of lipofuscin as a determinant of age is that metabolic rate, and hence lipofuscin accumulation rate, remains fairly constant over the portion of the life history of interest. The rainbow trout were reared in a hatchery where no net change in the environment occurred from 1983 to 1985. Dover sole, on the other hand, gradually migrate into deeper, colder, and less oxygenated waters as they age. Presumably the metabolism of fish under these conditions would be lower as might be the rate of lipofuscin accumulation in the brain.

The literature on fishes provide no conclusive evidence that lipofuscin is an accurate index of age over the entire lifespan. Hill and Radtke (in press) reported that the extracted lipofuscin per unit dry weight in the brain of the tropical fish *Dascillus albisella* accumulates exponentially with age. The relationship is driven by a single point for an 11-year-old individual and it would probably be linear without that single point, if only fish 1–7 years old were considered. In hatchery-reared *Cyprinus carpio* the total extracted lipofuscin per unit of dry weight in the brain of fish of the same age (6 years) increased with weight over 8-fold range in weight (Griven et al.[2]). About 45% of the lipofuscin content could be explained by difference in weight among fish. Thus, in fish of the same age there was a strong size effect on lipofuscin concentration. These results are very similar to those found in this study. Aloj Totaro et al. (1985) found that lipofuscin increased over a range of 0–2 years. But the method was different as they measured lipofuscin granules present in the electric lobe of *Torpedo marmorata* brains rather than using extractable lipofuscin of the entire brain. Thus, all studies to date seem to indicate that accumulation occurs in the brains of fishes, but results are not conclusive owing to small sample sizes, limited age ranges, and failure to identify the effects of brain growth on rates of accumulation.

Additional research is required to evaluate lipofuscin as a method of age determination in fishes. The effect of brain growth on lipofuscin accumulation rates must be considered in such studies. A promising approach in this regard may be to estimate lipofuscin on a per cell basis instead of on a weight basis. This could be accomplished by either expressing extracted lipofuscin relative to DNA concentration or by histological techniques.

[2]Girven, R. J., R. W. Gauldie, Z. Czochanska, A. D. Woolhouse. Manuscr. in prep. A critical tests of the lipofuscin technique of age estimation in fish.

Acknowledgments

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Literature Cited

AGIUS, C., AND S. A. AGBEDE.
1984. An electron microscopical study on the genesis of lipofuscin, melanin, and haemosiderin in the haemopoietic tissues of fish. J. Fish Biol. 24:471–488.

ALOJ TOTARO, E., F. A. PISANTI, P. RUSSO, AND P. BRUNETTI.
1985. Evaluation of aging parameters in *Torpedo marmorata*. Ann. Soc. R. Zool. Belg. 115(2):203–209.

BLIGH, E. G., AND W. J. DYER.
1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37:911–917.

BOEHLERT, G. W.
1985. Using objective criteria and multiple regression models for age determination in fishes. Fish. Bull, U.S. 83:103–107.

DAPSON, R. W., A. T. FELDMAN, AND G. PANE.
1980. Differential rates of ageing in natural populations of old-field mice (*Peromyscus polionotus*). J. Gerontol. 35:39–44.

ETTERSHANK, G.
1984. A new approach to the assessment of longevity in the Antarctic krill *Euphausia superba*. J. Crustacean Biol. 4:295–305.

ETTERSHANK, G., I. MACDONNELL, AND R. CROFT.
1983. The accumulation of the age pigment by the fleshfly

Sarcophaga bullatta Parker (Diptera: Sarcophagidae). Aust. J. Zool. 31:131–138.

FLETCHER, B. L., C. J. DILLARD, AND A. L. TAPPEL.
1973. Measurement of fluorescent lipid peroxidation products in biological systems and tissues. Anal. Biochem. 52:1–9.

GULLAND, J. A.
1978. Analysis of data and development of models. *In* J. A. Gulland (editor), Fish population dynamics, Ch.4. Wiley.

HILL, K. T., AND R. L. RADTKE.
In press. Gerontological studies of the damselfish, *Dascyllus albisella*. Bull. Mar. Sci.

MACARTHUR, M. C., AND R. S. SOHAL.
1982. Relationship between metabolic rate, aging, lipid peroxidation, and fluorescent age pigment in milkweed bug, *Oncopeltus fasciatus* (Hemiptera). J. Gerontol. 37:268–274.

MIQUEL, J., P. LUNDGREN, AND J. E. JOHNSON, JR.
1978. Spectrofluorometric and electron microscopic study of lipofuscin accumulation in the testis of ageing mice. J. Gerontol. 33:5–19.

MULLIN, M. M., AND E. BROOKS.
1988. Extractable lipofuscin in larval marine fish. Fish. Bull., U.S. 86:407–415.

MUNNELL, J. F., AND R. GETTY.
1968. Rate of accumulation of cardiac lipofuscin in the ageing canine. J. Gerontol. 23:154–158.

NICOL, S.
1987. Some limitations on the use of the lipofuscin ageing technique. Mar. Biol. (Berl.) 93:609–614.

REICHEL, W.
1968. Lipofuscin pigment accumulation and distribution in five rat organs as a function of age. J. Gerontol. 23:145–153.

SHELDAHL, J. A., AND A. L. TAPPEL.
1973. Fluorescent products from aging *Drosophila melanogaster*: an indicator of free radical lipid peroxidation damage. Exp. Gerontol. 9:33–41.

SMITH, P. J.
1987. Homozygous excess in sand flounder, *Rhombosolea plebeia*, produced by assortive mating. Mar. Biol. (Berl.) 95:489–492.

SOHAL, R. S., AND H. DONATO.
1978. Effects of experimentally altered life spans on the accumulation of fluorescent age pigment in the housefly, *Musca domestica*. Exp. Gerontol. 13:335–341.

STREHLER, B. L., D. D. MARK, A. S. MILDVAN, AND M. V. GEE.
1959. Rate and magnitude of age pigment accumulation in the human myocardium. J. Gerontol. 14:430–439.

TAPPEL, A. L.
1975. Lipid peroxidation and fluorescent molecular damage to membranes. *In* B. F. Trump and A. V. Arstila (editors), Pathobiology of cell membranes, Vol. 1. Acad. Press, N.Y.

ZAR, J. H.
1974. Biostatistical analyses. Prentice-Hall, Englewood Cliffs, NJ, 620 p.

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EXTRACTABLE LIPOFUSCIN IN LARVAL MARINE FISH

The "age pigment", lipofuscin, is thought to be a biochemically heterogeneous byproduct of the peroxidation of polyunsaturated lipids which accumulates in dense, intracellular inclusions called ceroid bodies. The material has been studied both microscopically and biochemically in tissues of several species (Miquel et al. 1977; Shimasaki et al. 1980; Dowson 1982), and some portion of it is quantitatively extractable with organic solvents (Fletcher et al. 1973).

Flies prevented from flying by putting baffles in the bottles in which they were raised, accumulated lipofuscin (as assessed by solvent extraction) more slowly than did free-flying flies but had a longer lifespan, so that at the ends of the respective lifespans the body contents of lipofuscin were similar in the two groups (Sohal and Donato 1978). Extractable lipofuscin thus appears to accumulate as a function of cumulative oxidative metabolism; it could be an indicator of physiological (rather than strictly chronological) age.

Additionally, if lipofuscin represents an integral of oxidative metabolism since birth and weight represents an integral of growth over the same period, the ratio of lipofuscin to organic weight should be proportional to the reciprocal of cumulative net growth efficiency [K_2 = growth/assimilation = growth/(growth + respiration), hence $1/K_2 = 1 +$ respiration/growth].

Ettershank (1984a) introduced the fluorometric measurement of extractable lipofuscin as a measure of physiological age in growing marine crustaceans, based on the work with insects, and (1984b) recommended a simple method for routine use in marine work. He also argued (without presenting extensive evidence) that preservation

of tissue in formalin-seawater did not invalidate the analysis; thus, historical samples of zooplankton (and, presumably, larval fish) appeared to be usable for study of intraspecific geographic or interannual variability.

Although most studies of lipofuscin (especially by histology) have concerned postmitotic cells, such as nervous tissue, we evaluated the assay as an estimate of the relative efficiency of growth of larvae analyzed whole. That is, we were less interested in lipofuscin as an indicator of age (for which, as we show, other measures of mass are useful) than as an indicator of health whose relation to mass would reflect environmental conditions over time. We therefore investigated the importance of interfering fluorescing pigments (Csallany and Ayaz 1976), tested the effect of preservation in formalin (Nicol 1987), and measured the accumulation of extractable lipofuscin in three species of larval fish reared in the laboratory—California grunion, *Leuresthes tenuis*; white seabass, *Atractoscion nobilis*; and California halibut, *Paralichthys californicus* (hereafter referred as grunion, seabass, and halibut respectively).

Analytical Considerations

We analyzed lipofuscin by a method first described by Fletcher et al. (1973), as modified by Ettershank (1984b). The tissue to be analyzed (usually whole larvae) was frozen (−15° or −70°C) and later freeze-dried, and a 1–5 mg sample was homogenized in at least 2 mL of 2:1 chloroform:methanol in a Wheaton glass tissue homogenizer. After extracting for 3–4 hours at 4°C, 100 mM $MgCl_2$ (25% of the solvent volume) was added, and the solutions were thoroughly mixed and then centrifuged for 20 minutes at 3000 rpm at −4°C. The lower, chloroform layer was withdrawn for fluorometric analysis after reaching 20°C in a water bath, and the fluorescence was measured on a Turner 111[1] fluorometer using a CS 7–60 filter (approximately 360 nm) for excitation and a CS 47B filter (approximately 430 nm) for emission. A known concentration of quinine sulfate was the standard, and results are therefore reported as "fluorescence units" or FU/mg.

A stock solution of quinine sulfate (2 mg/L in 1 N H_2SO_4) was stored in a light-tight reagent bottle. To compare analyses done at different times, sets of standards were prepared from this stock in distilled water (0.02, 0.04, 0.06, 0.08, and 0.10 μg/mL). Some of the sets prepared over a year's time are shown in Figure 1; the overall reproducibility is good.

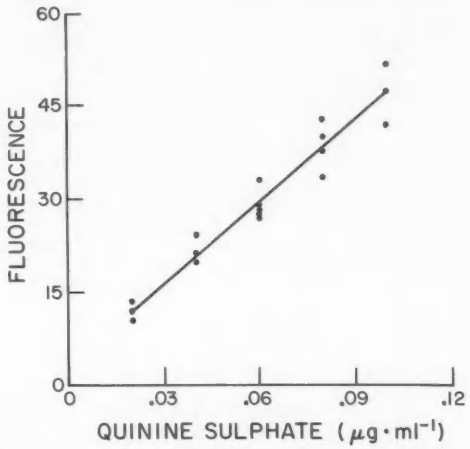


FIGURE 1.—Reproducibility of different sets of quinine sulfate standards prepared from a stock solution over a year.

Precision of the method, including extraction from tissue, was estimated by comparing replicate samples of liver and white muscle from adult halibut. The coefficients of variation for 5 determinations on each of 3 sets of tissue were for muscle, 0.2, 0.35, and 0.57, and for liver, 0.1, 0.15, and 0.18. The difference in variability between the two kinds of tissues is probably due to the greater difficulty in homogenizing muscle tissue.

Quinine sulfate standards were compared on a Farrand Spectrofluorometer, with excitation at 350 nm and emission at 420 nm, and on the Turner 111 fluorometer. The correlation coefficient for measurements on the two instruments was 0.97. We therefore used the Turner 111 routinely, so that analyses could be done easily in a hood.

Csallany and Ayaz (1976) described interference by retinol in the analysis of organic-solvent-soluble lipofuscin in mammalian tissues, and recommended a chromatographic step to remove this contaminant. We extracted a variety of fish tissues in 2:1 chloroform:methanol, and after addition of $MgCl_2$ and centrifugation, dried the chlo-

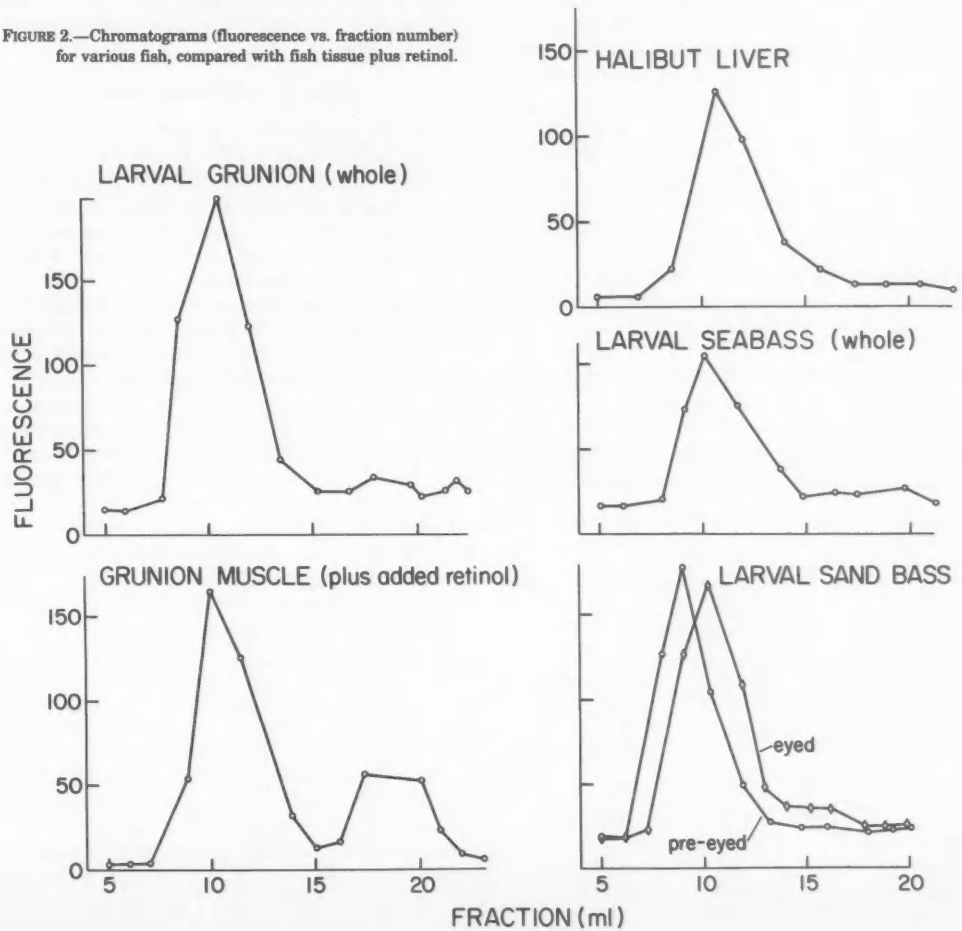
[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

roform layer gently (35°C) in an open vial overnight in a hood on a sand bath. The dried extract was reconstituted with 1:9 chloroform:methanol and chromatographed on a 30 cm Sephadex LH20 column at a flow rate of 3–4 mL/hour. A fraction was collected by hand every 20 minutes, its volume measured, and its fluorescence determined on the Turner 111 at the same wavelengths used for routine analysis of lipofuscin. To determine where a retinol peak would appear, we chromatographed a tissue extract to which a commercial preparation (Sigma) of retinol had been added. Also, extracts of larval fish in the pre-eyed stage were compared with extracts of larvae that had pigmented eyes, assuming that the eyed larvae would have more retinol.

A UV irradiation step had been proposed to degrade retinol where it may interfere with measurement of extracted lipofuscin, but Csallany and Ayaz (1976) reported that this procedure was ineffective. We therefore determined the time course of degradation of commercial retinol in 1:9 chloroform:methanol by UV irradiation in quartz tubes.

At the wavelengths we used, retinol was not an important interfering substance in a variety of larval fish and in the adult grunion muscle and adult halibut liver tissues (Fig. 2). There also was little difference between extracts of eyed and pre-

FIGURE 2.—Chromatograms (fluorescence vs. fraction number) for various fish, compared with fish tissue plus retinol.



eyed larvae. We therefore did not use UV irradiation routinely. If UV irradiation is used to degrade retinol, the exposure must be kept short (1 or 2 minutes), or else another compound fluorescing at these wavelengths appears (Fig. 3), giving the spurious impression that UV did not affect retinol; this may explain the negative results of Csallany and Ayaz (1976).

To evaluate the effect of preservation in formalin, we froze subsamples from stocks of larvae, and preserved other subsamples in 10% formalin in a glass container, using formalin from a glass reagent bottle. We analyzed frozen and preserved larvae after 3 months, and after an additional year we analyzed more preserved larvae.

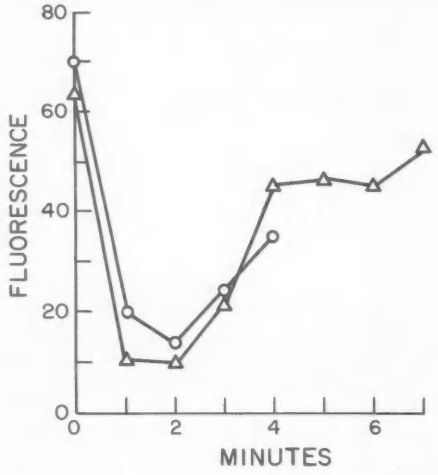


FIGURE 3.—Time course of fluorescence resulting from UV irradiation of duplicate batches (two symbols) of retinol.

Nicol (1987) recently demonstrated that formalin preservation significantly increases the fluorescence of lipofuscin extracted in chloroform-methanol, and our results show similar analytical problems (Table 1). There was significant enhancement in fluorescence in the larvae preserved for over a year, when compared with those preserved for 3 months. Quinine sulfate standards run at the same time as the samples for different periods were very similar (Fig. 4), indicating real changes with time of preservation. Thus, this method will not permit using historical collections of formalin-preserved animals to determine their relative physiological states until more is known about the time course and nature of the effect of formalin on the extract of preserved tissue.

Larval Growth Experiments

Seabass larvae were obtained from Hubbs Research Institute and halibut larvae from the Los Angeles County Natural History Museum; larval grunion were obtained by stripping adults and bringing fertilized eggs into the laboratory for hatching in an aerated, 10 L container of seawater at room temperature.

Larval grunion were reared in 40 L Nalgene tubs with spigots at the bottom (which facilitated emptying and cleaning), initially stocked with 100–120 newly hatched grunion per tub, with replicated "high" and "low" food concentrations. Larvae were fed newly hatched *Artemia* nauplii and the rotifer, *Brachionus*, which was cultured on *Dunaliella tertiolecta* in 100 L, lighted

TABLE 1.—Lipofuscin (as fluorescence units, FU) per animal and per unit dry weight (DW) of frozen vs. formalin-preserved larval fish. N = number of larvae per analysis.

	Frozen (3 months)		Preserved (3 months)		Preserved (1 year)	
	FU (larva)$^{-1}$	FU (mg DW)$^{-1}$	FU (larva)$^{-1}$	FU (mg DW)$^{-1}$	FU (larva)$^{-1}$	FU (mg DW)$^{-1}$
Grunion	16.0	47.4	24.3	60.1	44.3	98.1
N = 15	16.7	47.3	31.0	76.7	45.0	93.1
	17.3	47.7	23.6	60.4	48.0	100.1
	17.0	49.7	24.0	63.0	54.3	112.7
			26.0	65.3	51.0	106.2
$\bar{X}$ =	16.8	48.0	25.7	65.3	48.5	102.0
Seabass	0.68	18.6	0.82	13.6	1.72	22.3
N = 30	0.47	13.0	0.71	12.0	2.05	26.3
	0.50	14.5	0.46	8.0	2.03	27.2
	0.43	12.7	0.52	8.7	1.63	22.2
	0.33	9.4	0.60	10.5	2.05	28.9
$\bar{X}$ =	0.48	13.6	0.62	10.6	1.89	25.4

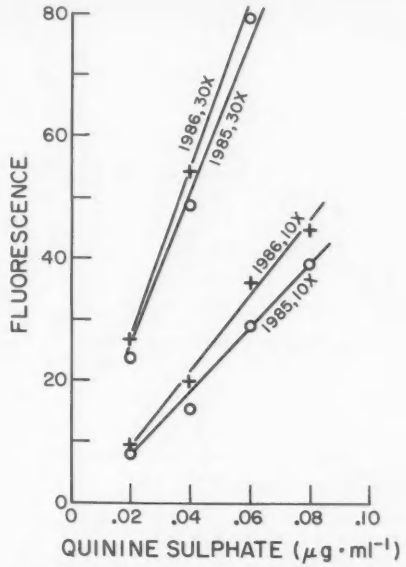


FIGURE 4.—Fluorescence of various concentrations of quinine sulfate standards read at 10× gain (lower pair of lines) and 30× gain (upper pair) in 1985 (lower line of each pair) and 1986 (upper of each pair).

polyethylene tubs augmented with f/2 phytoplankton nutrients (May 1971; Theilacker and McMaster 1971). One spring and one summer experiment were completed at ambient temperatures (spring = 17.5°–19°C, summer = 21°–23°C), with one of the "high food" containers in the second experiment kept at 26°C with an aquarium immersion heater.

We were unable to maintain absolute high and low food concentrations because of oscillations in the supply of food organisms. Thus, the high concentration was kept at 3 times the low concentration, although absolute amounts varied. The mean initial food concentrations in the spring experiment were 50 μg C/L (= "low") and 154 μg C/L (= "high"); in summer, 122 and 394 μg C/L, respectively. Tubs were censused every 2 days through each experiment to determine how much food was uneaten and how many larval fish had died (estimated by counting and removing corpses), and to add fresh food. In the low food containers, it was not unusual to find little uneaten food, particularly as the larvae grew. Once a week the tubs were emptied and the remaining larvae counted directly. It was clear from this direct census that all dead larvae were not accounted for by searching for corpses every 2 days because of cannibalism, necrophagy, or decay. Every 4 days a known number of larvae was removed; their lengths were measured and they were frozen for future analyses.

We could not estimate larval ingestion precisely because of the uncertainty in how many fish were alive through a 2-d interval. This problem was exacerbated as the larvae within each tub diverged in size, so that variance in individual ingestion increased. Although 3 times more food was offered in the high food containers, these larvae actually ingested about twice the amount of food as did those in the low food containers (Table 2). This difference was due to better survival in the high food containers, which affected the ratio between available ration and number of larvae. To compensate for this, we routinely harvested more animals from the high food containers than from the low food containers.

Freeze-dried animals or tissues were weighed on a Cahn electrobalance. Protein was determined by a method of Dorsey et al. (1977) on an aliquot of tissue homogenized in cold 1 M NaCl. DNA was measured by an ethidium bromide technique (Bentle et al. 1981, as modified by M. S. Lowrey). Basic measures of size—dry weight, protein, and DNA—were strongly and linearly correlated (Fig. 5), so that comparing lipofuscin with any of these measures would give similar patterns.

Lipofuscin accumulated as the larval fish grew (Fig. 6), but at quite different rates for the 3 species, grunion accumulating most rapidly (relative to gain in weight) and seabass much the slowest.

TABLE 2.—Estimated average ingestion, size, composition, and growth efficiency for 20-day-old, laboratory-reared larval California grunion. Compare with Figure 5.

	Spring experiment		Summer experiment	
	Low food	High food	Low food	High food
μg C ingested[1] per individual	701	1,723	1,379	2,792
μg dry weight per individual	755	1,305	901	1,895
μg DNA per mg protein	84.8	59.4	48.1	31.3
μg C[2] per individual	245	603	482	977
Growth from hatching (μg C)	104	462	341	836
Gross growth efficiency	15%	27%	25%	30%

[1]Calculated from measured carbon in *Brachionus* and *Artemia*.
[2]Estimated from literature values.

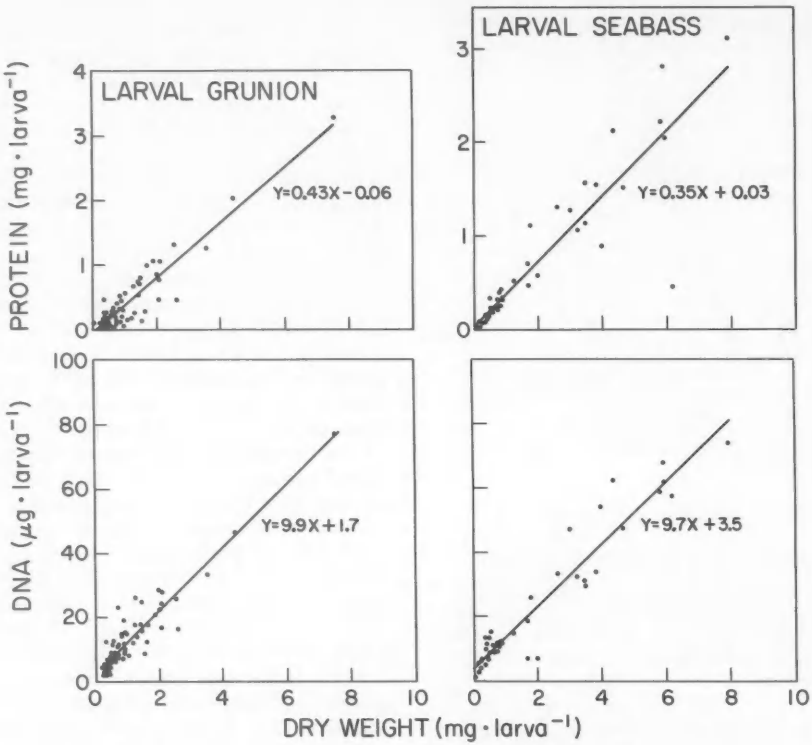


FIGURE 5.—Relations of protein (upper) and DNA (lower) to dry weight for laboratory-reared larval grunion (left) and white seabass (right).

This may reflect differences in the lifespans and metabolic rates; grunion are small fish, reaching maturity in a year and living less than 5 years (Frey 1971), while seabass and halibut grow to very much larger size and can live more than 20 years (Frey 1971; Thomas 1968).

Figure 7 shows the variability in the amount of lipofuscin in larvae of the same age. At time "0", all fish were newly hatched. The variance was low in the first few days, but increased dramatically with time because larvae within each tub grew (and, presumably, respired) at very different rates. There were differences in averages between high food and low food conditions, and between experiments (Table 2), but the variance in dry weight, protein, DNA, or lipofuscin was so large that the overlap obscured any differences between conditions of rearing.

Grunion and halibut larvae start life with greater concentrations of lipofuscin than do seabass, and though the concentration decreases rapidly as grunion and halibut age (Fig. 8), they still have almost a 10-fold greater concentration than do larval seabass when all are 20 days old. All three species increased in weight faster than they increased in lipofuscin, so the concentration of lipofuscin was "diluted" by growth. Because protein was a constant fraction of dry weight (Fig. 5, upper), this dilution was not due to skeletal growth alone. If the rate of weight-specific growth exceeds the rate of weight-specific respiration during early life, the concentration of lipofuscin should decrease, as observed, and only when growth ceases or slows considerably should lipofuscin accumulate relative to weight. Alternatively, lipofuscin could change chemically with time, becoming more difficult to extract (Vernet et al. 1988), so that the rate of accumulation of lipofuscin would be underestimated.

We attempted to stop growth by starving the

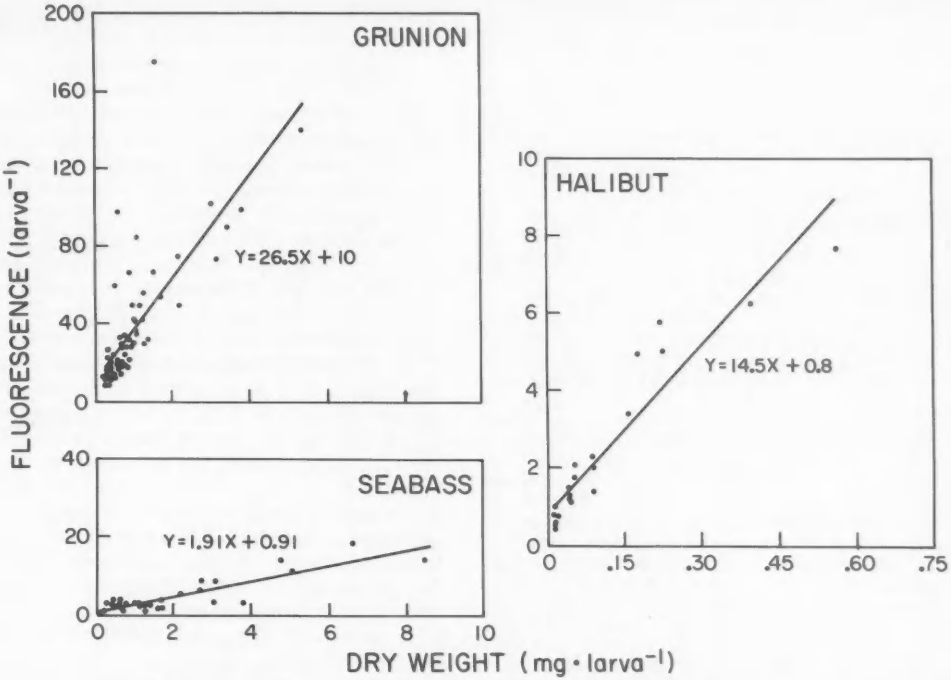


FIGURE 6.—Relation of lipofuscin fluorescence per larva to dry weight for larval grunion (upper left) white seabass (lower left), and California halibut (right). Note different axes.

larvae to see if we could detect an increase in lipofuscin. Table 3 shows results for seabass starved for the final 20% of the rearing period; there was no significant change in the concentration of lipofuscin. This is not what one would expect if accumulation of lipofuscin is proportional to physiological age, unless no lipid is metabolized during starvation. However, this result also could reflect slow transformation of lipofuscin from a more to a less soluble pool (Vernet et al. 1988).

TABLE 3.—Lipofuscin fluorescence (FU) per unit dry weight of larval white seabass starved for various periods after age 29 days. *N* = number of analyses; ranges in parentheses.

	FU (mg dry weight)$^{-1}$	*N*
Initial		
29 days old	2.4 (1.6–3.0)	4
Starved		
2 days	3.1 (2.3–4.0)	2
4 days	1.3 (0.54–1.7)	6
6 days	1.8 (1.4–2.3)	2
8 days	2.5	1

Conclusions

Our intent was to evaluate the utility of measuring extracted lipofuscin fluorometrically as an indicator of the integrated metabolic health of fish, especially preserved ones, and of relative net efficiency of growth. We conclude that this technique is unlikely to be useful in these ways, at least within the larval period. Although the accumulation of total body burden of lipofuscin was demonstrated, the variability among individuals grown under the same conditions became so large over time that we were unable to calibrate the method in an ecologically meaningful sense. The variability was evident in all measures of growth,

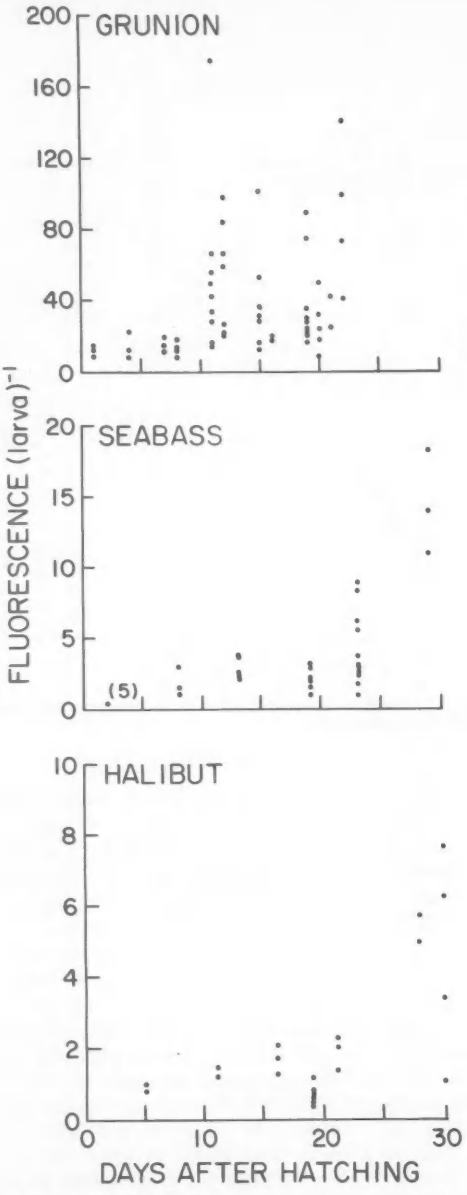


FIGURE 7.—Lipofuscin fluorescence per larva vs. age since hatching for laboratory-raised larval grunion (top), white seabass (center), and California halibut (bottom).

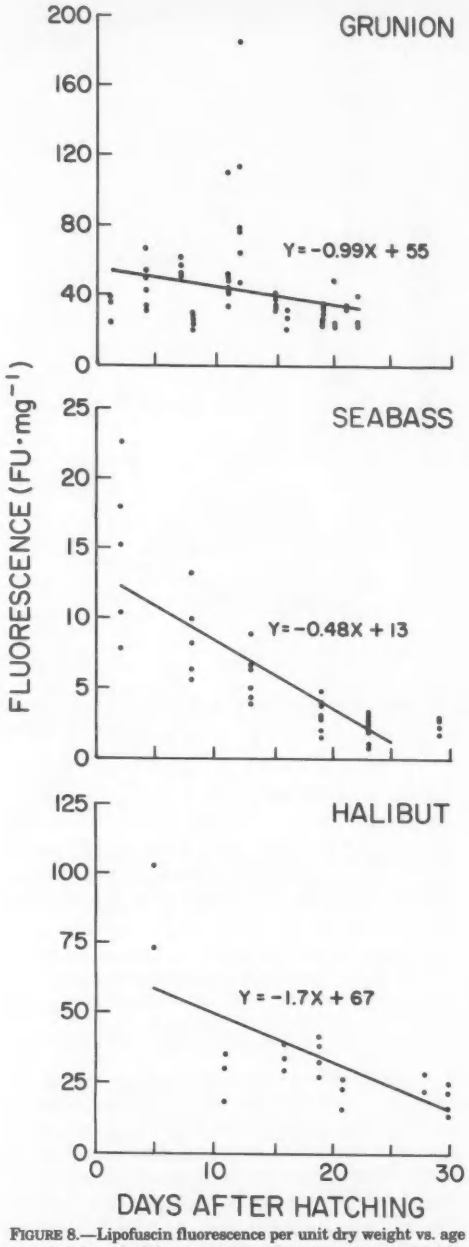


FIGURE 8.—Lipofuscin fluorescence per unit dry weight vs. age since hatching for laboratory-reared larval grunion (top), white seabass (center), and California halibut (bottom). Linear fits are for comparative purposes only; relations for seabass and halibut look curvilinear.

and is common in culture of larval fishes. Such variability may be reduced in nature, where runts may be subject to intense predation.

Lipofuscin analysis may be useful only when applied to postmitotic tissue, such as nervous tissue in mature fish, or to whole organisms whose mitotic growth has essentially ceased, such as adult copepods or insects (since the methods appear useful in arthropods—Ettershank et al. 1983; Sohal and Donato 1978). In these organisms, the vagaries of growth are reduced, and the accumulation of lipofuscin during starvation or exercise might show that lipofuscin concentration is interpretable as a measure of physiological age, habitat quality, and net growth efficiency.

Lipofuscin is known to be a polytypic substance, probably variable in composition among different organisms. We have assumed that a constant proportion of the same substance is extracted. This may not be true (Vernet et al. 1988), and considerable work remains to be done on the basic biochemistry of the component substance(s). Though the extraction and fluorometric measurement is tantalizingly simple, it may well be that the microscopical method used to quantify "ceroid bodies" is the best approach. Fluorescent techniques used in histochemical research (Brizzee and Jirge 1981), combined with automatic imaging procedures, might decrease the tedium of staining and visual microscopy.

Acknowledgments

We thank Refik Orhun and Steve Cadell for the larval white seabass and halibut, and Maria Vernet and two referees for helpful comments. Research was supported by California Department of Fish and Game project C-921 and National Science Foundation grant OCE86-00742.

Literature Cited

BENTLE, L. A., S. DUTTA, AND J. METCOFF.
1981. The sequential enzymatic determination of DNA and RNA. Anal. Biochem. 116:5–16.

BRIZZEE, K. R., AND S. K. JIRGE.
1981. Fluorescent microscope techniques for the visualization and histological quantification of autofluorescent lipofuscin bodies in brain tissues. *In* J. E. Johnson (editor), Current trends in morphological techniques, Vol. III. CRC Press.

CSALLANY, A. S., AND K. L. AYAZ.
1976. Quantitative determination of organic solvent soluble lipofuscin pigments in tissue. Lipids 11:412–417.

DORSEY, T. E., P. W. MCDONALD, AND O. A. ROELS.
1977. A heated Biuret-Folin protein assay which gives equal absorbance with different proteins. Anal. Biochem. 78:156–164.

DOWSON, J. H.
1982. The evaluation of autofluorescence emission spectra derived from neuronal lipopigment. J. Microsc. 128:261–262.

ETTERSHANK, G.
1984a. A new approach to the assessment of longevity in the Antarctic krill *Euphausia superba*. J. Crust. Biol. 4(Spec. No. 1):295–305.
1984b. Methodology for age determination of Antarctic krill using the age pigment lipofuscin. Biomass Handb. No. 26. SCAR/SCOR/IABO/ACMRR.

ETTERSHANK, G., I. MACDONNELL, AND R. CROFT.
1983. The accumulation of age pigment by the fleshfly *Sarcophaga bullata* Parker (Diptera: Sarcophagiidae). Aust. J. Zool. 31:131–138.

FLETCHER, B. L., C. J. DILLARD, AND A. L. TAPPEL.
1973. Measurement of fluorescent lipid peroxidation products in biological systems and tissues. Anal. Biochem. 52:1–9.

FREY, H. W.
1971. California's living marine resources and their utilization. Calif. Dep. Fish Game, Resour. Agency, 148 p.

MAY, R. C.
1971. Effects of delayed initial feeding on larvae of the grunion *Leuresthes tenuis* (Ayres). Fish. Bull., U.S. 69:411–425.

MIQUEL, J., J. ORO, K. G. BENSCH, AND J. E. JOHNSON, JR.
1977. Lipofuscin: fine-structural and biochemical studies. *In* W. A. Pryor (editor), Free radicals in biology, p. 133–182. Acad. Press, N.Y.

NICOL, S.
1987. Some limitations on the use of the lipofuscin ageing technique. Mar. Biol. (Berl.) 93:609–614.

SHIMASAKI, H., N. VETA, AND O. S. PRIVETT.
1980. Isolation and analysis of age-related fluorescent substances in rat testes. Lipids 15:236–241.

SOHAL, R. S., AND H. DONATO.
1978. Effects of experimentally altered life spans on the accumulation of fluorescent age pigment in the housefly, *Musca domestica*. Exp. Gerontol. 13:335–341.

THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as food for larval anchovies. Mar. Biol. (Berl.) 10:183–188.

THOMAS, J. C.
1968. Management of the white seabass (*Cynoscion nobilis*) in California waters. Calif. Dep. Fish Game, Fish. Bull. 142, p. 1–34.

VERNET, M., J. R. HUNTER, AND R. D. VETTER.
1988. Accumulation of age pigments in two cold-water fishes. Fish. Bull., U.S. 86:401–407.

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NOTICES

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ERRATA

Fishery Bulletin: Vol. 86, NO. 1

Butler, John L., and Darlene Pickett, "Age-specific vulnerability of Pacific sardine, *Sardinops sagax*, larvae to predation by northern anchovy, *Engraulis mordax*," p. 163–167.

Pages 165 and 166 have incorrect figures for the legends, please replace with the following:

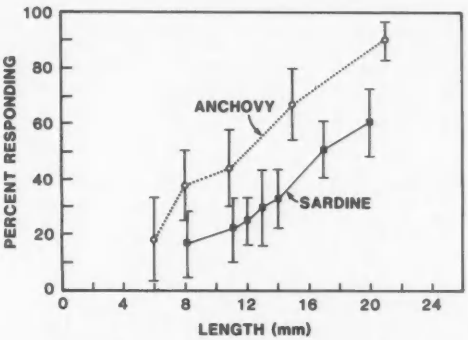

FIGURE 1.—Increase by size of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, responding to attack by adult northern anchovy and 95% confidence intervals. Data on anchovy larvae from Folkvord and Hunter (1986).

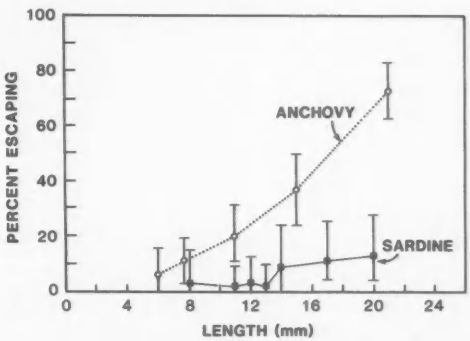

FIGURE 3.—Increase by size of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, escaping attack by adult northern anchovy and 95% confidence intervals. Data on anchovy larvae from Folkvord and Hunter (1986).

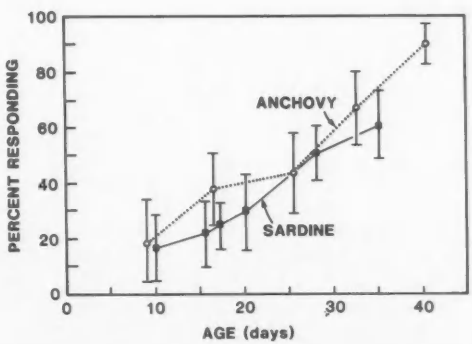

FIGURE 2.—Increase by age of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, responding to attack by adult northern anchovy and 95% confidence intervals. Size categories of reared larvae have been converted to ages using growth rates estimated from the field. Data on anchovy larvae from Folkvord and Hunter (1986).

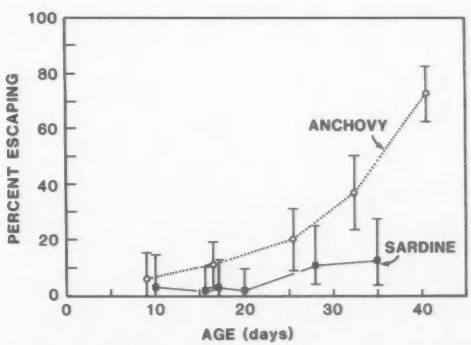

FIGURE 4.—Increase by age of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, escaping attack by adult northern anchovy and 95% confidence intervals. Size categories of reared larvae have been converted to ages using growth rates estimated from the field. Data on anchovy larvae from Folkvord and Hunter (1986).

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WATSON, CHERYL, ROBERT E. BOURNE, and RICHARD W. BRILL. A computer-based theory on the etiology of burnt tuna 357
BROWN-PETERSON, NANCY, PETER THOMAS, and CONNIE R. ARNOLD. Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in South Texas 375

Notes

CHEN, CHE-TSUNG, TZYH-CHANG LEU, and SHOOU-JENG JOUNG. Notes on reproduction in the scalloped hammerhead, *Sphyrna lewini*, in northwestern Taiwan waters 389
COLLINS, MARK R., and CHARLES A. WENNER. Occurrence of young-of-the-year king *Scomberomorus cavalla*, and Spanish, *S. maculatus*, mackerels in commercial shrimp trawls along the Atlantic coast of the southeast United States 394
DEW, C. BRAXTON. Stomach contents of commercially caught Hudson River striped bass, *Morone saxatilis*, 1973–1975 397
VERNET, MARIA, JOHN R. HUNTER, and RUSSELL D. VETTER. Accumulation of age pigments (lipofuscin) in two cold-water fishes 401
MULLIN, M. M., and E. R. BROOKS. Extractable lipofuscin in larval marine fish 407
Notices. NOAA Technical Reports published during the last 6 months of 1987 416